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A Critical Checklist of the Ants of Mongolia (Hymenoptera: Formicidae)

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Abstract. Here we present a critical species list of the ants of Mongolia, that is based on current literature, previously unpublished taxonomic changes, the unpublished records of the zoological expeditions of Japanese-Mongolian and German-Mongolian teams in the years 1997, 1999 and 2003 and the results of a four year Polish-German-Mongolian cooperation. We report on 68 species of 17 genera of ants that have been found within Mongolia: *Camponotus*, *Cardiocondyla*, *Cataglyphis*, *Crematogaster*, *Dolichoderus*, *Formica*, *Harpagoxenus*, *Lasius*, *Leptothorax*, *Messor*, *Myrmica*, *Plagiolepis*, *Polyergus*, *Proformica*, *Tapinoma*, *Temnothorax* and *Tetramorium*. Six species are new to Mongolia: *Formica pressilabris* Nylander, 1846, *Lasius gebaueri* Seifert, 1992, *Myrmica commarginata* Ruzsky, 1905, *Myrmica kamtschatica* Kupyanskaya, 1986, *Myrmica eidmanni* Menozzi, 1930 and *Myrmica taediosa* (Bolton, 1995).

Keywords. Asia, Mongolia, Formicidae, species list.

1. INTRODUCTION

Mongolia occupies several natural zones where the Siberian taiga forest meets the Central Asian steppe and the Gobi desert. Steep gradients of temperature and moisture show opposing trends and run contrary from North to South resulting in a vegetation sequence of forest, steppe, semi desert and desert that is considerably influenced by different soil conditions and altitudinal changes. This complex set of parameters, together with the large area of the country, creates a large variety of habitats and has a distinct influence on the biodiversity of the region (EMELJANOV & KERZHNER 1983; WALTER 1983; BRECKLE et al. 1994). Ants are a dominant part of the ground-dwelling Mongolian entomofauna, and form distinct communities in the different biomes and vegetation zones of this country (PFEIFFER et al. 2003).

The ant fauna of Central Asia has been studied for more than a century (e.g., MOCSÁRY & SZÉPLIGETI 1901), however, either these early expeditions did not occur on the territory of today's Mongolia (RUZSKY 1905; STITZ 1934; YASUMATSU 1940), or other authors had caste doubt on the validity of the determinations (e.g., DLUSSKY 1965 on RUZSKY 1915, and PISARSKI 1969a on FOREL 1904 and MOCSÁRY & SZÉPLIGETI 1901). Basic information on the Mongolian ant fauna has been gathered by the Hungarian entomologist Dr. Z. KASZAB, whose collections from the 1960s were identified by DLUSSKY (1965), DLUSSKY & PISARSKI (1970), PISARSKI (1969 a,b) and PISARSKI & KRZYSZTOFIAK (1981). DLUSSKY (1964, 1967, 1969), RADCHENKO (1994b,c, 1995a, 1997a, 2005) and SEIFERT (2000, 2003, 2004) provided additional information on the ant species composition of the Mongolian fauna and were focused to the taxonomic editing of the species (for details see below). PFEIFFER et al. (2003, 2004) obtained the first ecological research data that revealed the biogeographical patterns of the Mongolian ant fauna. Here we present a preliminary checklist of the ants of Mongolia based on a critical evaluation of older literature and on the results of our own expeditions.

2. MATERIALS AND METHODS

Our study is based on altogether 2145 samples from 174 locations that were accumulated in Mongolia between 1997 and 2004 (Fig. 1). We collected ant specimens during several expeditions to the Gobi desert and the steppe and forest zones of this country. Additionally several hundred specimens of other collections were taxonomically evaluated by A. Radchenko and B. Seifert.

Three German Mongolian expeditions were conducted by M. Pfeiffer and K. Ulykpan: the first together with L. Chimedregdzen from July to September 1997, the second in July/August 1999 and the third together with A. Ulykpan in July/August 2003. They collected 703 samples mostly from baits at 67 locations in 1997 and 1999, including 11 sites that have been sampled most intensively (see PFEIFFER et al. 2003), and about 200 samples of a larger investigation at altogether 37 locations in 2003. All specimens were collected from several North-South transects between E95° and E118° longitude all over Mongolia. M. Woyciechowski collected 262 samples from *Myrmica* nests within four years (1999, 2000, 2001, and 2002) in the forest steppe zone in the Hentii region (North Mongolia). Ants from nests were collected in all types of vegetation (MÜHLENBERG et al. 2000) around and between three main locations stretched across ca 100 km along the 49th parallel: Honin Nuga Research Station (N49°04'48", E107°17'15"), Hot springs (N49°01'08", E107°32'43") and Ming River valley (N49°00'06", E108°02'36"). The Japanese-Mongolian expedition of Sk. Yamane and A. Ulykpan accumulated 2200 ant specimens from 233 samples from colonies and general collection that were sampled in June and July 2003, in Bogd Han National Park, Hustai N.P., and Terelj N.P. (all Tuv aimag); in Zamyn uud (Dornogovi aimag) and in July 2004 in Bogd Han N.P.; in Honin Nuga, and in Han Hentii Mts. (Selenge aimag). R. Schultz sampled the western part of Mongolia in July and August 2003 on an expedition from Ulaanbaatar through Hangai Mts. to Hovd and the Mongolian Altai (Hovd aimag) and examined 255 nest samples collected from 47 sites. He added more data to our list by the evaluation of 1) the collection of the University of Halle (77 samples from 7 locations), which was mainly due to the work of Mrs. Dr. A. Stubbe and 2) of the diploma thesis of A.-L. Lucau (2004), who collected 145 samples of the same three sites that had also been collected by M. Woyciechowski (Honin Nuga Research Station, Hot springs and Ming River valley) and was supervised by Prof. Dr. M. Mühlenberg, University of Göttingen.

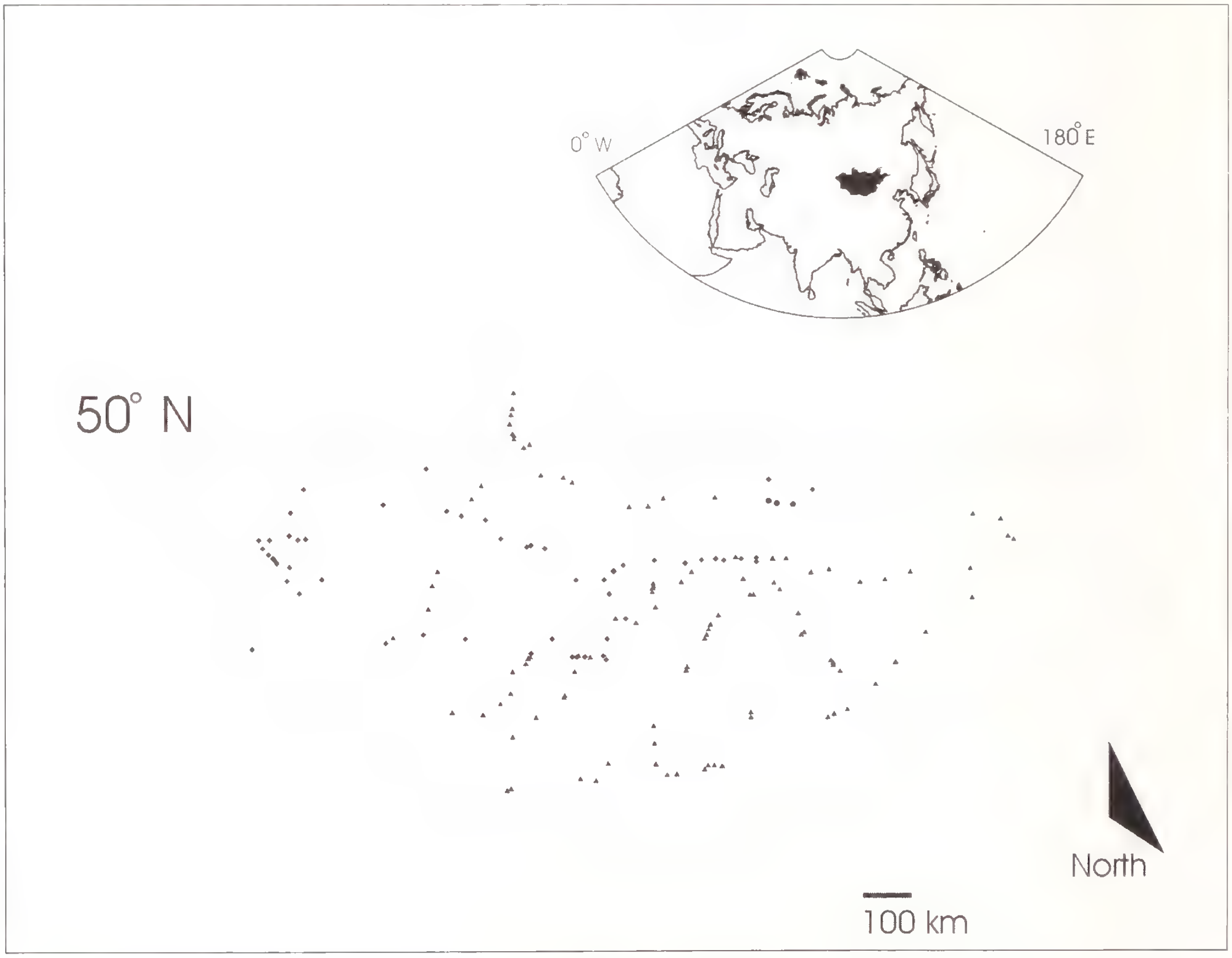

Fig. 1. Map of Mongolia. Given are the positions of our sample sites. The world map in the upper right corner shows the geographical position of Mongolia (black) in the centre of Asia.

If not explicitly stated otherwise, the material that we have collected during these journeys was identified by Alexander Radchenko (genera *Camponotus*, *Cataglyphis*, *Crematogaster*, *Messor*, *Myrmica*, *Plagiolepis*, *Proformica* and *Temnothorax*), Bernhard Seifert (genera *Cardiocondyla*, *Formica*, *Lasius* and *Polyergus*), Graham-W. Elmes (*Myrmica*) and the other authors. Collection details and localities for all species will be given in future publications, in which we plan to map the distribution patterns of the main species.

To compile the species list we compared our data with that in the literature (see Table 1 and references). These references were critically scrutinized by our taxonomic experts (B. Seifert, A. Radchenko) and the validity of the nomenclature was checked by evaluating the latest taxonomic publications (BOLTON 1995, 2003; RADCHENKO 1994a,b, 1995b,c, 1997a,b; RADCHENKO et al. 2002; SEIFERT 1992, 2000, 2003, 2004).

3. RESULTS

The resulting list of the Mongolian fauna comprises 68 species of ants of 17 genera (Table 1). After cross checking of literature we conclude that six species are new to the Mongolian fauna (R. Schultz, Sk. Yamane & M. Woyciechowski, unpubl. results):

***Formica pressilabris* Nylander, 1846**
Hangai mountain region, Arhangai aimag (province), Tsetserleg soum, ca. 12 km west of Tsetserleg, 1886 m, leg. R. Schultz, 02.08.2003, det. B. Seifert.

***Lasius gebaueri* Seifert, 1992**
Tuv aimag: Bogd Han N.P., 1550 m, leg. Sk. Yamane, 27.06.2003, det. B. Seifert.

Mongolian Altay, Hovd aimag, ca. 8 km south of Hovd, ca. 20 km west of Hovd, 2021 m, leg. R. Schultz, 08.08.2003, det. B. Seifert.

***Myrmica commarginata* Ruzsky, 1905**
Hovd aimag, Durgun soum, Chonoharaihiin gol, Derris, 1154 m, leg. A. Stubbe, 27.08.2003, det. R. Schultz & A. Radchenko.

***Myrmica eidmanni* Menozzi, 1930**
Selenge aimag, western Han Hentii Mts, 3 km SW from Honin Nuga Research Station, near Eruu River (N49°03.81', E107°16.14'), 930 m, 06.08.1999 and 8 km E from Honin Nuga Research Station, near Sharlan River (N48°57.70', E107°04.26'), 970 m, 23.07.2000, both leg. M. Woyciechowski, det. G. W. Elmes & A. Radchenko.

Selenge aimag, western Han Hentii Mts, Sharlan River, near Honin Nuga research station, 1000 m, leg. A.-L. Lucau, July 2001, det. A. Radchenko.

Selenge aimag, western Han Hentii Mts, Sharlan River, near Honin Nuga research station, leg. Sk. Yamane, July 2004, det. Sk. Yamane.

***Myrmica kamtschatica* Kupyanskaya, 1986**
Selenge aimag, western Han Hentii Mts, 8 km E from Honin Nuga Research Station, near Sharlan River (N48°57.70', E107°04.26'), 970 m, leg. M. Woyciechowski, 23.07.2000 and the same location on 6.07.2001, det. G. W. Elmes & A. Radchenko.

***Myrmica taediosa* (Bolton, 1995)**
Selenge aimag, western Han Hentii Mts, 9 km SW from Honin Nuga Research Station, near Eruu River (N49°02.39', E107°11.62'), 1045 m, leg. M. Woyciechowski, 28.07.2002, det. G. W. Elmes & A. Radchenko.

Due to taxonomic changes and to our critical evaluation of the species lists that have been previously published, this first comprehensive list of the Mongolian ant fauna contains a changed species spectrum compared to the older literature. For example *Lasius alienus* (Förster, 1850) has been reported from Mongolia in four publications (DLUSSKY & PISARSKI 1970; PISARSKI 1969a,b; PISARSKI & KRZYSZTOFIAK 1981), however, regarding to SEIFERT (1992), this species is constricted to Europe, so the taxonomic position of these samples was doubtful. A rechecking of these specimens that had been collected by Kaszab and are housed in the Hungarian National Museum showed that they were most possibly specimens of *Lasius* cf. *obscuratus*, but definitively not of *Lasius alienus* (Sándor Csõsz, Budapest, pers. comm. 2005). *Lasius* cf. *obscuratus* has been also sampled by PFEIFFER (2003) but due to the low number of specimens this determination is still uncertain and needs to be confirmed.

Other records that have been previously published are also uncertain and may be a result of misidentifications (unpublished results A. Radchenko): e.g., *Camponotus herculeanus herculeanus* Linnaeus, 1758 (in DLUSSKY & PISARSKI 1970), *Cardiocondyla stambuloffi* Forel, 1892 (in PISARSKI 1969b; PISARSKI & KRZYSZTOFIAK 1981, but see RADCHENKO 1995c and SEIFERT 2003), *Myrmica bergi* Ruzsky 1902 that was confirmed to be *Myrmica divergens* Karavaiev, 1931 (in PFEIFFER et. al. 2003, but see RADCHENKO et al. 2002), *Myrmica saposhnikovi* Ruzsky, 1903 (in PISARSKI 1969a,b, PISARSKI & KRZYSZTOFIAK 1981), that was proved to be *M. pisarskii* Radchenko, 1994 (see RADCHENKO 1994b, 1995b), and *Myrmica schencki* Viereck, 1903 (in PISARSKI & KRZYSZTOFIAK 1981), which

Table 1. A critical list of the ant species that have been found in Mongolia, according to literature, to our expeditions and the expertise of our taxonomic experts A. Radchenko and B. Seifert. a = Stitz (1934), b = Holgersen (1943), c = Dlussky & Pisarki (1970), d = Dlussky 1965, e = Pisarski (1969a), f = Pisarski (1969b), g = Pisarski & Krzysztofiak (1981), h = Radchenko (1994b), j = Radchenko (1994c), k = Radchenko (1995a), l = Bolton (1995), m = German-Mongolian expedition 1997; 1999 (collection M. Pfeiffer, unpublished), n = collection of Kawaguchi, o = Radchenko (1997a), p= Dubatolov (1998), q = collection of M. Woyciechwski (1999–2004), r = collection of R. Schultz (leg. A.-L. Lucau 2001, 2003), s= collection of R. Schultz (leg. University of Halle, Germany), t = Imai et al. (2003), u= Pfeiffer et al. (2003), v = German-Mongolian expedition 2003 (M. Pfeiffer), w = German-Mongolian expedition 2003 (R. Schultz), x = Seifert 2003, y = Japanese-Mongolian expedition 2003 (Sk. Yamane), z = Japanese-Mongolian expedition 2004 (Sk. Yamane), 1 = Seifert (2004), 2 = Radchenko (2005), 3 = Personal collection A. Ulykpan. Valid scientific names were obtained from Bolton 1995, 2003; Radchenko 1994 a,b, 1995b,c, 1997 a,b; Radchenko et al. 2002 and Seifert 2000, 2003, 2004.

Scientific name	References
Camponotus japonicus Mayr, 1866	b,c,e,f,g,s,y,z,3
Camponotus herculeanus sachalinensis Forel, 1904	c,e,f,g,w,y,z,3
Camponotus saxatilis Ruzsky, 1895	m,o,w,z,
Camponotus turkestanus André, 1882	f,g,s,u,v
Cardiocondyla koshewnikovi Ruzsky, 1902	u,w,x
Cataglyphis aenescens (Nylander, 1849)	c,e,f,g,s,u,v,w
Crematogaster subdentata Mayr, 1877	g,u
Dolichoderus sibiricus Emery, 1889	2
Formica aquilonia Yarrow, 1955	e,n,v,y, z
Formica candida Smith, 1878	c,d,e,f,g,n,r,s,u,v,w,y,z,1,3,
Formica clara Forel, 1886	c,f,u,v,y
Formica clarissima Emery, 1925	s,u,w
Formica cunicularia Latreille, 1798	c,f,g,3
Formica exsecta Nylander, 1846	d,m,w,y,z
Formica forsslundi Lohmander, 1949	c,e,f,g,w,3
Formica japonica Motschoulsky, 1866	t
Formica kozlovi Dlussky, 1965	d,e,f,g,m,w,y,3
Formica lemani Bondroit, 1917	c,d,f,g,m,w,y,z,3
Formica lugubris Zetterstedt, 1838	f,w,y z,
Formica manchu Wheeler, 1929	c,d,e,f,g,l,m,n,s,w,y,z,3
Formica pisarskii Dlussky, 1964	d,e,f,g,v,w,y,3
Formica pratensis Retzius, 1783	c,d,f,s,3
Formica pressilabris Nylander, 1846	w
Formica sanguinea Latreille, 1798	c,d,e,f,g,s,u,y,z,3
Formica truncorum Fabricius, 1804	c,d,f,3
Formica uralensis Ruzsky, 1895	c,d,e,f,g,u,w,y,3
Harpagoxenus zaisanicus Pisarski, 1963[1]	e,f,g,3
Lasius distinguendus (Emery, 1916)	e,f,3
Lasius flavus (Fabricius, 1781)	b
Lasius gebaueri Seifert, 1992	w,y,z,3
Lasius niger (Linnaeus, 1758)	b,c,f,g
Lasius przewalskii Ruzsky, 1915	g,w,y,z,3
Leptothorax acervorum (Fabricius, 1793)	e,f,g,w,3
Leptothorax muscorum (Nylander, 1846)	c,e,f,g,y,3
Messor aciculatus (Smith, 1874)	e,f,u,y
Messor excursionis Ruzsky, 1905	g
Myrmica angulinodis Ruzsky, 1905	c,e,f,g,r,w,q,y,z,3
Myrmica arnoldii Dlussky, 1963	c,e,g,r,q,y,z,3
Myrmica commarginata Ruzsky, 1905	s
Myrmica divergens Karavaiev, 1931	c,e,g,w,q,y,z,3
Myrmica eidmanni Menozzi, 1930	q,r,z

Myrmica forcipata Karavaiev, 1931	e,f,g,r,w,q,3
Myrmica kamtschatica Kupyanskaya, 1986	q
Myrmica kasczenkoi Ruzsky, 1905	c,e,f,g,v,w,y,3
Myrmica koreana Elmes, Radchenko & Kim 2001	u,q
Myrmica pisarskii Radchenko, 1994	h,s,u,w,q,y,3
Myrmica rubra (Linnaeus, 1758)	b,k
Myrmica ruginodis Nylander, 1846	k,q
Myrmica sulcinodis Nylander, 1846	e,f,r,q,3
Myrmica taediosa Bolton, 1995	q
Plagiolepis manczshurica Ruzsky, 1905	e,f,g,u
Polyergus nigerrimus Marikovsky, 1963	p,u
Proformica buddhaensis Ruzsky, 1915	f,g,u
Proformica coriacea Kuznetsov-Ugamsky, 1927	f
Proformica jacoti (Wheeler, 1923)	g,w
Proformica kaszabi Dlussky, 1969	u
Proformica mongolica (Emery, 1901)	c,e,f,g,u,w
Tapinoma orthocephalum Stitz, 1934[2]	a
Tapinoma sinense Emery, 1925	j
Temnothorax kaszabi (Pisarski, 1969)	f,g,3
Temnothorax melleus (Forel, 1904)	f
Temnothorax mongolicus (Pisarski, 1969)	f,u,v,z
Temnothorax nassonowi (Ruzsky, 1895)	e,f,g,u,y
Temnothorax serviculus (Ruzsky, 1902)	c,e
Tetramorium armatum Santschi, 1927	g,u
Tetramorium concaviceps Bursakov, 1984	u
Tetramorium inerme Mayr, 1877	f,u
Tetramorium tsushimae Emery, 1925	c,e,f,g,u,w,y

[1] This species is on the red list of Mongolia (http://www.redlist.org).

[2] This species has been reported from South Mongolia, but it is unclear whether this place is now in the Peoples Republic of China.

in fact is *M. koreana* Elmes, Radchenko & Kim 2001. Other mistakes seem to be most probably *T. caespitum* Linnaeus, 1758 (in Dlussky & Pisarski 1970; Pisarski 1969b), that may be *Tetramorium tsushimae* Emery, 1925 and also *Tetramorium ferox* Ruzsky, 1903 (in Pisarski & Krzysztofiak 1981). Similarly, Dlussky & Pisarski (1970) and Pisarski (1969b) reported about *Formica polyctena* Förster, 1850 to occur in Mongolia's forest steppe, however, this seems to be a misidentification of specimens of *Formica aquilonia* Yarrow, 1955 (B. Seifert, pers. obs.). Because of the cold winter the occurrence of *F. polyctena* within Mongolia should be impossible. We excluded all suspicious records from our species list.

Due to the failure to access type material of *Formica subpilosa ruzskyi* Dlussky 1965, only indirect assessment of the status of this taxon is possible. Most certainly this taxon is conspecific with *F. clarissima* Emery, 1925 because any material known from Mongolia and Tibet seems to belong to one and the same species according to structural characters. Furthermore there is no indication that those pigmentation characters proposed by the Dlussky (1965) for the differentiation of the *Formica subpilosa* subspecies *pamirica* Dlussky 1965, *clarissima* Emery 1925 (to which Dlussky applied the unnecessary replacement name *ruzskyi* Dlussky 1965) or *litoralis* Kuznetzov-Ugamsky 1926 could have any practical value. However, structural characters such as body morphometrics or setae counts computed in a discriminant analysis allow the separation of four Asian allospecies *Formica subpilosa* Ruzsky 1902, *F. clarissima* Emery 1925, *F. litoralis* Kuznetzov-Ugamsky 1926 and *F. pamirica* Dlussky 1965 (B. Seifert, unpubl. data). According to the material investigated by us only *F. clarissima* Emery 1925 could be confirmed for Mongolia. The possible occurrence of *F. subpilosa* in semideserts of S Mongolia, as extension of the population from Chinese Gobi desert, should be checked during further field studies. Similarly *Cataglyphis aenescens roickingeri* and *C. aenescens tankrei* have been synonymized with *C. aenescens* (Nylander, 1846) (Radchenko 1997b).

Table 2. Valid names of Mongolian ants and their former names or junior synonymies that have been used in the older literature.

Valid name	Former name
Cataglyphis aenescens (Nylander, 1846)	*Cataglyphis aenescens roickingeri* For *C. aenescens tankrei* For
Formica manchu Wheeler, 1929	*F. longiceps* Dlussky, 1964
F. dlusskyi Bolton, 1995	
Formica candida Smith, 1878	*F. picea* Nylander, 1846, sensu Dlussky 1967; sensu Dlussky & Pisarski 1971, and other authors *F. transkaucasica* Nassonov, 1889, sensu Collingwood 1979, and other authors
Temnothorax kaszabi (Pisarski, 1969)	*Leptothorax kaszabi* Pisarski, 1969
Temnothorax melleus (Forel, 1904)	*Leptothorax melleus* Forel, 1904 *Leptothorax melleus csikii* Pisarski, 1969
Temnothorax mongolicus (Pisarski, 1969)	*Leptothorax mongolicus* Pisarski, 1969 *Leptothorax serviculus mongolicus* Pisarski, 1969
Temnothorax nassonovi (Ruzsky, 1895)	*Leptothorax nassanovi* Ruzsky, 1895
Temnothorax serviculus (Ruzsky, 1902)	*Leptothorax serviculus* Ruzsky, 1902
Tetramorium tsushimae Emery, 1925	*Tetramorium annectens* Pisarski. 1969 *Tetramorium jacoti* Wheeler, 1927

In several cases the names of the species have been changed since that time when Dlussky and Pisarski identified the ant species from Kaszab's rich collection of the Mongolian fauna. For example *Formica manchu* Wheeler, 1929 was formerly named *F. longiceps* Dlussky, 1964 or *F. dlusskyi* Bolton, 1995 (see Seifert 2000) or *T. tsushimae* Emery, 1925 formerly considered as *Tetramorium annectens* Pisarski, 1969 or *Tetramorium jacoti* Wheeler, 1927 (see Bolton 1995). In the case of *Formica candida* Smith, 1878 this ant taxon was divided into two different species with separate zoogeography (Seifert 2004): the western "Black Bog Ant" redescribed as *Formica picea* Nylander, 1846, and *F. candida*, which is found in East Siberia from the eastern Altai mountains up to the Russian Far East, in Tibet, Mongolia, and North Korea. With these redescriptions the older name *Formica transkauscasica* Nassonov, 1889 that has been used for *F. candida*, e.g., in Pfeiffer et al. (2003), is invalid. Similarly some species of the genus *Leptothorax* have been transferred to the genus *Temnothorax* (e.g., *Temnothorax mongolicus* (Pisarski, 1969) or *Temnothorax nassonovi* (Ruzsky, 1895) (Bolton 2003). We excluded all synonymies (see Table 2) from the list.

4. DISCUSSION

For the first time we present a critical, tentative species list of the Mongolian Formicidae that includes all previously recorded taxa. We also added six new species, *F. pressilabris*, *L. gebaueri*, *M. commarginata*, *M. eidmanni*, *M. kamtschatica* and *M. taediosa* to the ant species list of Mongolia. Up to now the genus *Formica* provides the highest number of species (18) in this list, while *Myrmica* is represented by 14, *Lasius*, *Proformica* and *Temnothorax* by five species, each. The large number of *Formica* and *Myrmica* ants, that dominate the northern parts of Mongolia, may be a hint towards the higher productivity of these regions (forest, steppe) compared to the semi deserts and deserts in the southern country. However, the study of the Mongolian Formicidae is still going on, and we are expecting that more species will be added to the list within the next years (e.g., social parasitic ants), because of new collections and/or changes in the taxonomic system.

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The Life Cycle of *Lithobius mutabilis* L. Koch, 1862 (Myriapoda: Chilopoda)

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Abstract. The post-embryonic development and life cycle of *Lithobius mutabilis* L. Koch, 1862 were studied. Data for stage analyses were obtained by laboratory breeding and continuous observations of field-collected specimens in captivity over more than five years. Developmental stages are described with respect to the following characters: number of legs (anamorphic stages only), head length and width, length and width of tergite 3, body length, biomass, number of coxal pores, ocelli, and antennal articles. All characters were measured on living individuals under CO_2-anaesthesia. Information concerning oviposition and egg development, onset of sexual dimorphism and maturity, stage duration and moulting activity, life span and mortality as well as observations on feeding behaviour are provided. The results are compared with those of other investigations on *L. mutabilis* and other lithobiid species.

Keywords. Post-embryonic development, morphological characters, bionomy, Lithobiidae.

1. INTRODUCTION

Centipedes are essential components of the predatory arthropod fauna. Because of their considerable suitability as indicators of ecological site conditions, Lithobiidae attract utmost attention. The use of species as biological indicators is based on the knowledge of its ecofaunistical behaviour, phenology and bionomical strategy. Studies on centipede bionomics are much rarer than those on millipedes. Life cycles and stage morphology are known from only 40 centipede species, among them some 20 Lithobiomorpha, whereas about 150 millipede species have been investigated. For practical reasons, attention should be paid firstly on common and frequent species, like *Lithobius mutabilis* in Central Europe, which plays an important role as a dominant epigeic predator especially in woodlands. Further, this species has the advantage that its life cycle has already been the subject of studies by ALBERT (1983a, b) and FRÜND (1983) in western Germany (Solling, Steigerwald), using field-collected individuals as well as laboratory breeding. The availability of data on the life cycle of *L. mutabilis* from other localities allows possible similarities and differences in pattern to be investigated. Comparisons are also made with the post-embryonic development of other *Lithobius* species.

Our knowledge on post-embryonic development of myriapods was outlined by VERHOEFF (1905, 1925) with the concepts of "anamorphosis" (moultings connected with increases of body segments and legs), "epimorphosis" (moultings cause only differentiations in certain characters but keep constant numbers of body segments and legs) and "hemianamorphosis" (both developmental pathways in succession). All Lithobiomorpha develop by hemianamorphosis: a juvenile hatches with a small number of segments and legs and develops by a series of moults. At each moult there is an increase of segments and legs until a defined number is reached (anamorphic development). Further moults only lead to a growth in body size and a modification of various structures without increase of segments (epimorphic development).

This study is mainly focussed on the post-embryonic development (breeding biology, development, attainment of maturity and life span) of *Lithobius mutabilis* L. Koch, 1862. This has been done by laboratory breeding and cultures over several years. Description of stages, of variation in some morphological characters (e.g., number of antennal articles, ocelli, coxal pores) and growth analyses occupies a large part of the present study.

2. MATERIALS AND METHODS

2.1. Field collections

A total of 184 individuals of *L. mutabilis* were collected by hand in a deciduous woodland in the Neiße Valley near Görlitz through all seasons in the course of seven years: (1992) 1993–1997 (1998). The animals were transferred to the laboratory for measurement and further rearing. To ascertain the stage of freshly captured adults, it was sometimes necessary to observe two or more moults to overcome the wide overlap of characters between stages.

2.2. Laboratory rearing

For rearing, I used closed plastic vessels measuring 6 x 12 x 6 cm with a ground-layer of gypsum (no soil or leaf litter). The vessels were kept in a climate chamber at a constant temperature of 16 °C, which is the preferred temperature under natural conditions (BAUER 1955; PFLEIDERER-GRUBER 1986). They were examined every second day (youngest juveniles every day) in order to record all moults and egg-laying or to remove dead or sick individuals. At the same time the animals were fed (with collembolans, pieces of earthworms, enchytraeids, *Tubifex*, and, additionally, green leaf pieces of indoor plants), vessels were cleaned and the gypsum layer was moistened. Normally, two to three field collected or laboratory-bred specimens that were individually distinguishable were kept in one vessel.

Seventy-seven juveniles hatched under laboratory conditions. They were immediately isolated and transferred to other vessels, in order to prevent them from being eaten by the parents.

2.3. Measurements

The following results are based on the analyses of all the material, regardless of whether it was laboratory reared or more or less freshly captured.

Body-length, length and width of head and tergite 3, biomass (total numbers of body measurements see Table 1); numbers of coxal pores, antennal articles and ocelli were measured using a stereo-microscope with 12.8–40 x magnification (at µm-precision) and an analytical balance (precision 0.1 mg), respectively. Dead individuals were not weighed.

All individuals were measured alive under CO_2-anaesthesia. To check all characters, 3 to 4 gas treatments (each for some seconds only) were necessary. The CO_2-method has two important advantages: firstly, it is not damaging, i.e., it is possible to follow the development of one individual by measuring it after each moult; secondly, measurements of the relaxed animal can be obtained in contrast to measurements in alcohol, where body parts are contracted or curled up. However, using living material has the disadvantage of restricting measurements to "coarse" characters due to the short anaesthesia period.

3. RESULTS

3.1. Analysis of post-embryonic developmental stages

Designation of stages. In the centipede literature there is still disagreement about counting and nomenclature of the stages defined by the moults. VERHOEFF (1905, 1925) called the 1st juvenile stage a "foetus", the 2nd a "larva prima", "larva secunda", etc. Some authors (e.g., PFLUGFELDER 1932; DOHLE 1969, 1986) emphasized that the post-embryonic stages of centipedes are not true larvae. They neither have distinct larval characters nor do they live under ecological conditions different from those of the adults. Nevertheless, most of the authors continue

Table 1. Total numbers of measurements taken at different stages (BL – body length, HL – head length, HW – head width, T3L – length of tergite 3, T3W – width of tergite 3, BM – biomass). To be read in conjunction with Figure 1.

Stage		BL	HL	HW	T3L	T3W	BM
I				9	8	9	–
II				9	7	7	–
III		34	37	36	34	36	–
IV		31	31	31	30	31	–
V		32	32	32	31	32	11
VI (1)		35	35	35	35	35	26
VII (2)	♂	17	18	18	18	18	17
	♀	19	20	20	20	18	14
VIII (3)	♂	14	16	16	16	16	13
	♀	17	17	17	17	17	15
IX (4)	♂	16	10	10	10	10	9
	♀	8	9	8	9	9	9
X (5)	♂	21	30	30	28	28	25
	♀	14	15	15	14	14	13
XI (6)	♂	40	44	43	43	43	41
	♀	19	24	24	24	24	23
XII (7)	♂	37	46	46	44	45	43
	♀	29	32	32	31	31	28
XIII (8)	♂	25	28	29	29	29	27
	♀	17	21	21	20	21	20
XIV (9)	♂	14	14	14	14	14	14
	♀	12	13	12	13	13	12
XV (10)	♂	8	9	9	9	9	8
	♀	13	13	13	13	13	13
XVI (11)	♂	5	5	5	5	5	4
	♀	3	3	3	3	3	3
XVII (12)	♂	3	4	4	4	4	3
	♀	4	4	4	4	4	4
XVIII (13)	♂	2	2	2	2	2	2
	♀	4	4	4	4	4	4
XIX (14)	♂	2	2	2	2	2	2
	♀	1	1	1	1	1	1
XX (15)	♂	1	1	1	1	1	1
Sum		**497**	**540**	**555**	**543**	**548**	**405**

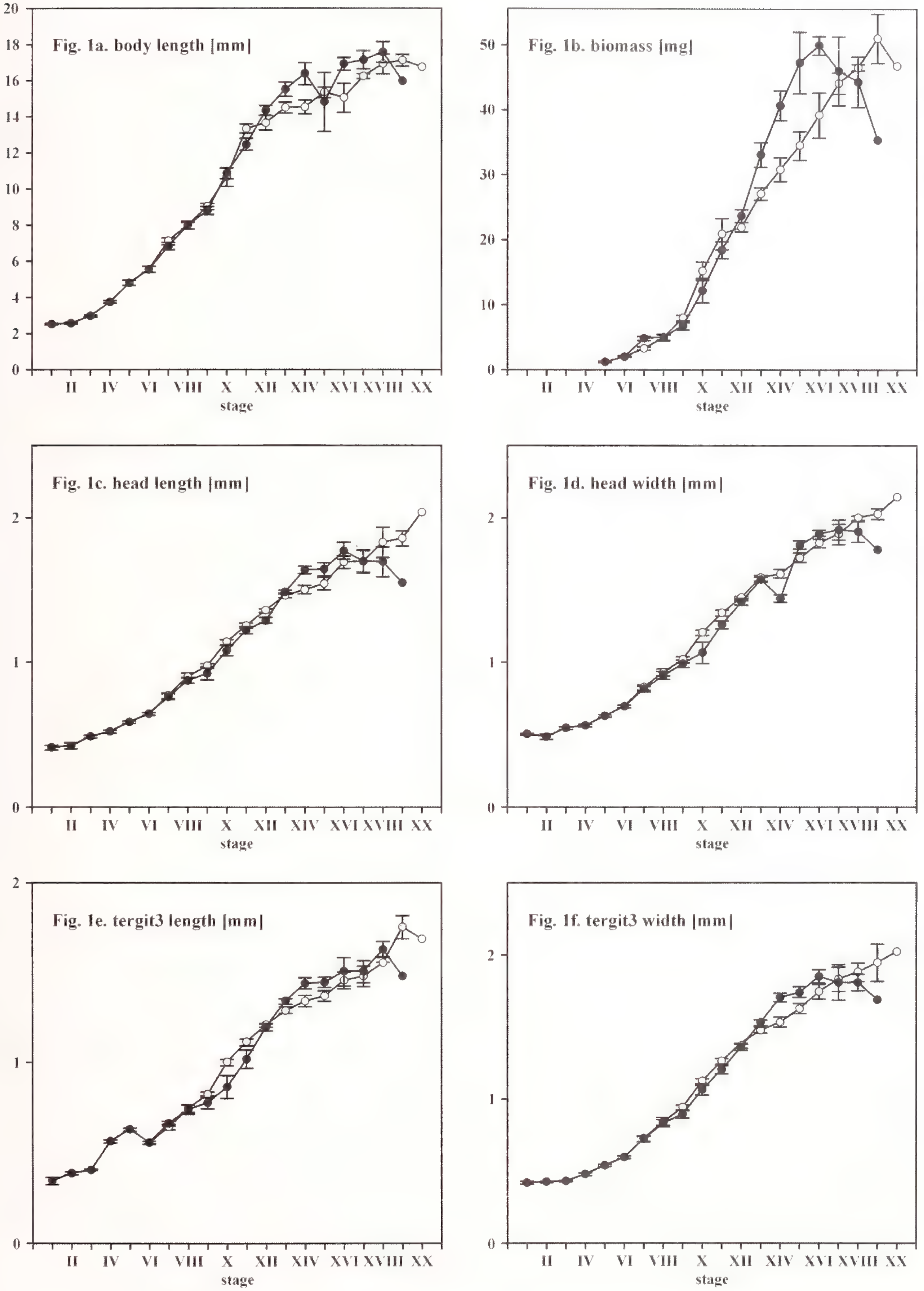

Fig. 1. Averages of body and biomass measurements of *L. mutabilis*. For numbers of measured specimens see Table 1; grey circles: males, black circles: juveniles and females.

Table 2. Comparison of different characters in epimorphic stages of *L. mutabilis* in the investigations from Neiße Valley (NV, present investigation), Steigerwald (St, Fründ 1982) and Solling (So, Albert 1982).

Stage		Sum of coxal pores of the leg pairs 12–15				Antennal articles			Number of ocelli		Head-width in mm			Body length in mm	
		NV		St		NV	St	So	NV	St	NV	St	So	NV	So
VI(1)	min.					18	24	22	3		0.57	0.58	0.66	4.13	
	mode	8		8		24	25		5	5	0.69	0.70	0.75	5.63	8.20
	max.					26	26	32	6		0.83	0.74	0.88	7.09	
VII(2)		♂j	♀j												
	min.	8	8	8		24	26	24	4	5	0.67	0.78	0.76	5.28	
	mode	12	16	11		28, 29	28		6	6	0.82	0.83	0.91	6.73	9.95
	max.	16	16	16		34	30	33	8	7	0.98	0.89	1.10	8.82	
VIII(3)	min.	14	16	13		26	29	30	5	6	0.59	0.89	0.86	7.00	
	mode	18	20	18		31	31		9	8	0.92	0.94	1.03	7.94	11.37
	max.	20	24	23		36	36	39	11	10	1.27	1.03	1.2	9.74	
IX(4)	min.	18	18	19		31	35	33	5	9	0.85	0.92	1.06	8.18	
	mode	22	22	23		34, 35	38		9	10	1.00	1,06	1.18	8.96	13.11
	max.	22	26	28		39	43	39	10	12	1.17	1.16	1.34	10.00	
X(5)	min.	24	22	23		31	36	36	7	9	1.00	1.07		9.50	
	mode	28	28	27		40	41		9	12	1.18	1.20	1.34	11.04	14.88
	max.	30	36	33		44	45	45	13	15	1.4	1.32		14.00	
		♂	♀	♂	♀										
XI(6)	min.	26	28	28	33	28	40		10	11	0.96	1.23		9.73	
	mode	32	34	32	37	39	43		12	14	1.31	1.35	1.47	13.01	16.36
	max.	38	38	36	44	44	48		13	17	1.56	1.47		15.50	
XII(7)	min.	30	30	28	35	30	40		9	13	1.07	1.35		11.14	
	mode	36	37	34	38	38–40	44		13	16	1.43	1.48	1.56	14.15	17.38
	max.	42	44	39	43	45	48		18	20	1.63	1.57		17.5	
XIII(8)	min.	32	36	32	36	33	41		9	14	1.37	1.54		12.08	
	mode	38	42	36	40	39	43		13	18	1.58	1.61	1.65	14.88	18.40
	max.	44	44	42	43	46	46		19	21	1.73	1.74		18.70	
XIV(9)	min.	34	38	37	45	33	40		12	19	1.46	1.64		13.63	
	mode	40	46	40	48	39	44		14	21	1.69	1.72	1.76	15.91	19.65
	max.	46	48	47	49	47	48		20	23	1.94	1.83		22.50	

to use the original terms of Verhoeff (Andersson 1976 ff.; Fründ 1983; Daas et al. 1996; Serra & Miquel 1996; Tuf 2002) and to call the anamorphic "larval" stages L0 –L4, and the epimorphic "post larval" stages PL 1, PL 2, Pl 3 etc. In the present study, the stages are designated (following Dohle 1986) by Roman numerals from first to last stage (I–XX). Additionally, the epimorphic stages are numbered in parentheses with Arabic numerals [(1– 15)].

A special problem was caused by Albert (1982) using the classification of stages created by Verhoeff (1905) without consideration that Verheoff's "agentilis" consists of two different stages (Brölemann 1930; Joly 1966; Lewis 1981). This mistake was corrected by Albert herself (Albert 1983b).

Determination and number of stages. The anamorphic period of the post-embryonic development of *L. mutabilis* comprises five stages, each terminated by a moult. Easily discernible morphological characters distinguish each stage.

Stage I. Seven pairs of legs and one pair of unbristled limb buds ("Beinanlagen"). The buds of legs 9 can be seen as small lateral bumps at the end of the body. The number of ocelli and antennal articles is 2 and 7, respectively, in all individuals investigated (Figs 3, 4).

Stage II. Eight pairs of legs, but legs 8 are incompletely developed and non-functional. All individuals have 11 antennal articles and 2 ocelli.

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[1] The number most frequantly is underlined..

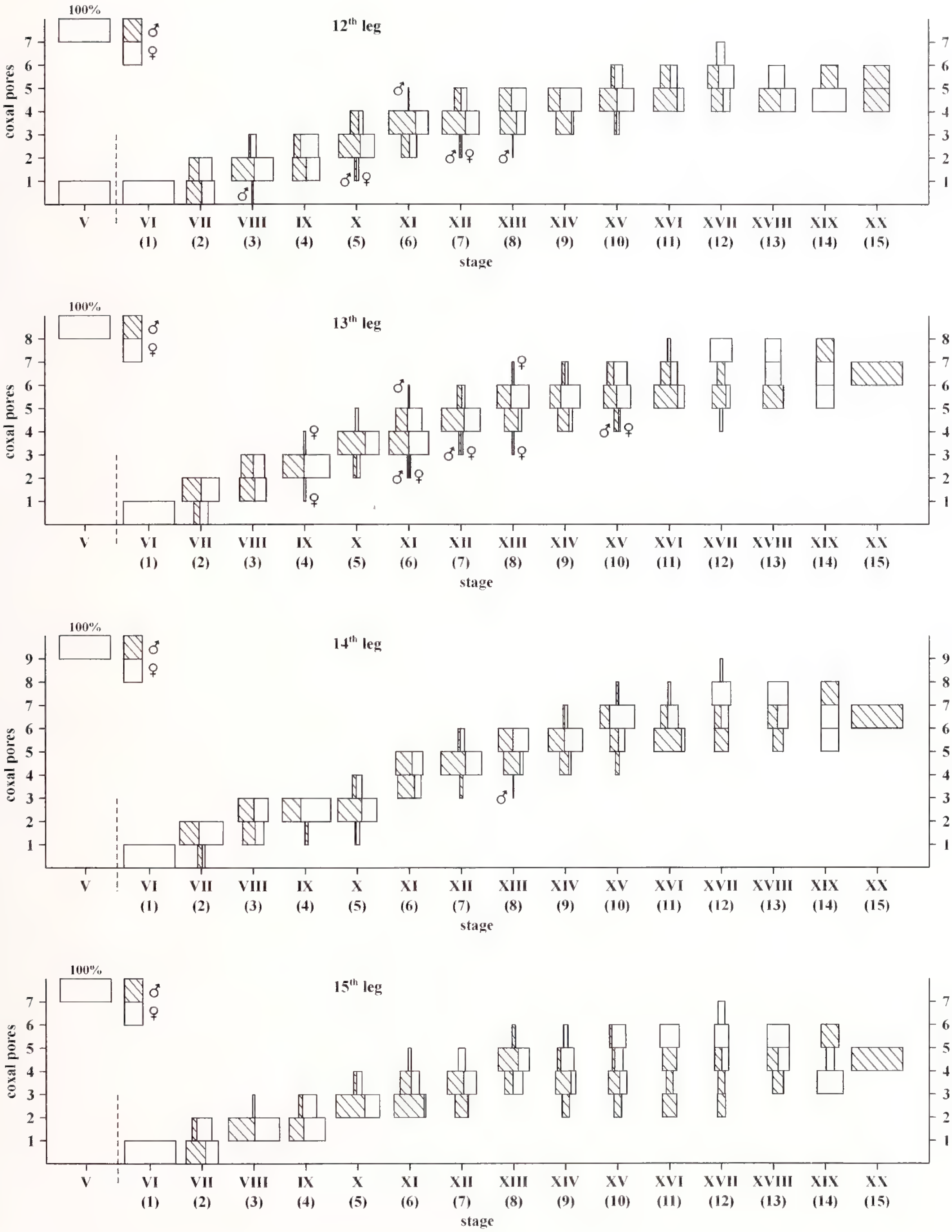

Fig. 2. Variation in numbers of coxal pores in different stages of *L. mutabilis*.

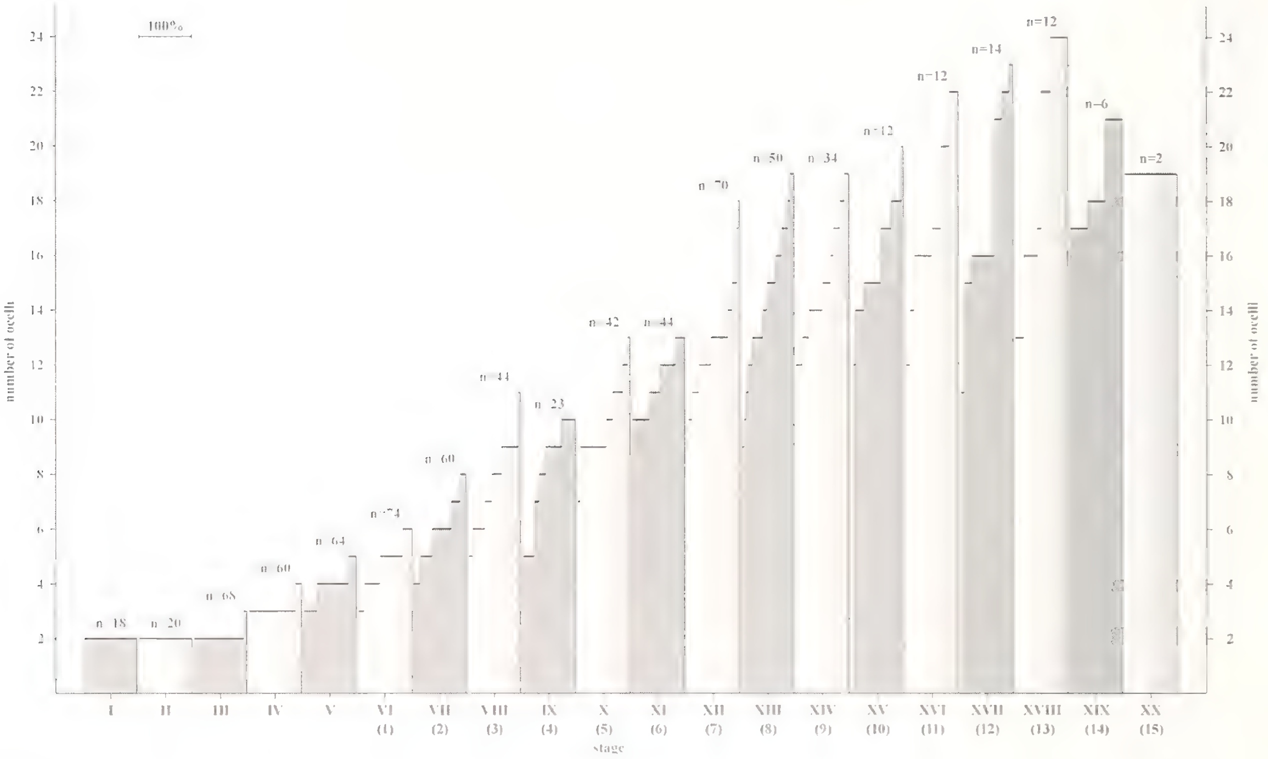

Fig. 3. Variation in numbers of ocelli in different stages of *L. mutabilis*, n: number of ocular fields counted.

Stage III. Eight fully developed pairs of legs and two pairs of limb buds; 14 antennal articles and 2 ocelli are characteristic for this stage. Very rarely 3 ocelli occur.

Stage IV. Ten pairs of legs and two pairs of limb buds. The number of antennal articles varies between 17, 18 and 19[1], the number of ocelli between 3 and 4.

Stage V (last anamorphic stage). Twelve pairs of legs and three pairs of limb buds, mostly with 23 antennal articles (16-23). The number of ocelli varies between 3, 4 and 5.

The first epimorphic stage VI (1) and all following stages have 15 functional pairs of legs. Therefore, other morphological characters (parameters of size as well as numbers of coxal pores, ocelli and antennal articles) must be used for determination of stages. The variability of these characters at each stage was determined for a better characterization of each stage.

The direct observation of all hatchings and the investigation of the development of different morphological characters during the life cycle of *L. mutabilis* in captivity led to the discovery of 15 epimorphic stages.

Growth analyses. The growth analyses show more or less sigmoid curves (Fig. 1) for all parameters, especially for body length, head length and width, and width of tergite 3. Up to stage V (the last anamorphic stage), there is a relatively small increase between each moult. With the next stage VI (1), relatively constant greater increments appear (linear curves) up to approximately stage XIV (9), where the curves become flatter again.

The differences between various stages are highly significant for all measurements for males and females, whereas the differences between males and females of the same stage are very rarely significant (Mann-Whitney-U test).

Number of coxal pores. The last anamorphic stage V of *L. mutabilis* has one coxal pore on its last leg (leg 12; Fig. 2). The following epimorphic stages have pores at the coxae of legs 12–15. Each moult can lead to an increase of 1 or 0 coxal pores per leg. On leg 12 there is never an increase of pores during the moult from stage V to stage VI (1). From 273 observed epimorphic moults only 6 (2%) occurred without any addition of pores at one of the four pairs of coxae. Figure 2 shows the combination of coxal pores in different stages and sexes of *L. mutabilis*.

Females have more coxal pores than males (Table 2). Figure 2 shows that the differences between the sexes are due

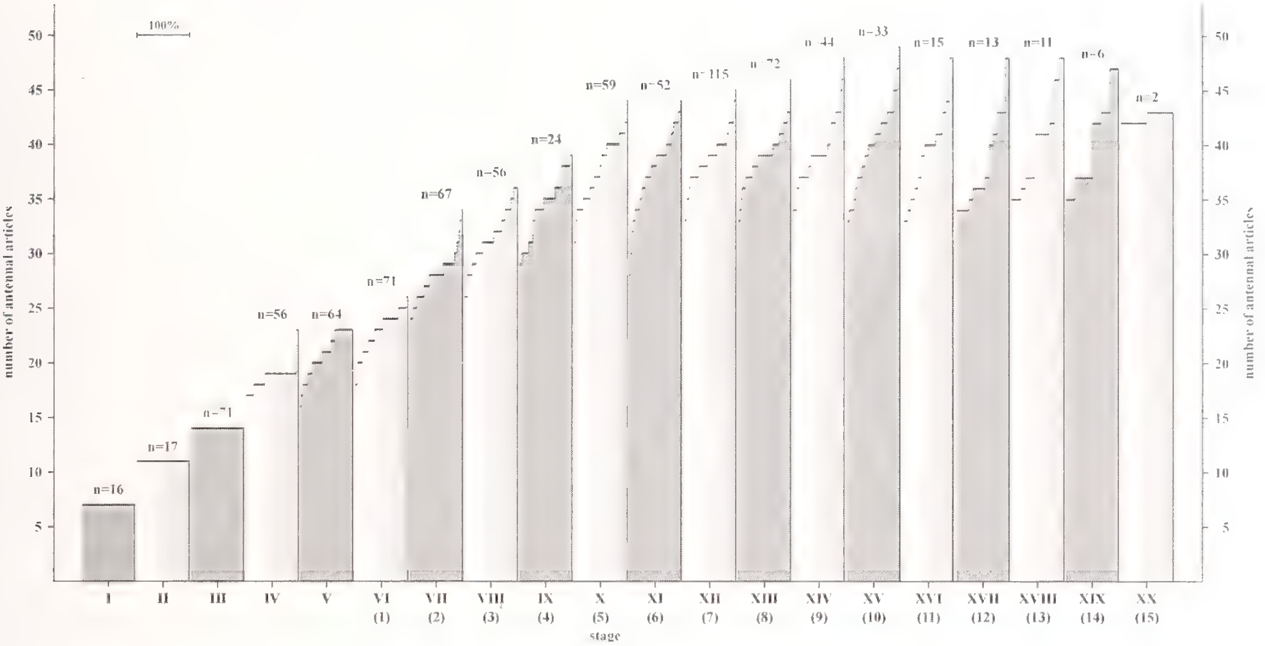

Fig. 4. Variation in antennal articles on each side in different stages of *L. mutabilis*, n: number of antennae counted.

to the lower number of coxal pores especially of leg 15 of males. In each stage there are certain preferred arrangements of increase. Overlaps of the preferred variants in males were between VIII (3) and IX (4), in females already between VII (2) and VIII (3). However, such overlaps apply to two stages only. In 16 % the left and right sides were different, but at most in one pore and on one leg only.

Number of ocelli. The first three stages have two ocelli on each side of the head. From stage IV onwards, the number of ocelli increases with each moult (Fig. 3). Variations begin with the (anamorphic) stage IV and become greater in later epimorphic stages. Within one stage, they can amount to as much as 12 ocelli. Thus, the overlap between different stages is very high. In both sexes, stage XVIII (13) with 24 ocelli has the highest observed number. The single male in the highest stage [XX (15)] had only 19 ocelli. No significant differences exist between males and females. Differences between the two sides of the head were rarely observed.

Number of antennal articles. The number of antennal articles increases during post-embryonic development from 7 to a maximum of 49 (Fig. 4). In the first three stages there is no variation in number. All studied antennae show 7, 11 or 14 articles, respectively. In stage IV, most individuals have antennae with 19 articles (with little variation). Beyond stage V, the number of antennal articles varies very widely within one stage. Also the left-right variability is very high (more than 50 %). In field-sampled individuals, it is often impossible to know whether a lower number results from an incomplete regeneration after loss of some articles.

In the first epimorphic stage VI (1), the usual numbers are 20 - 24 - 25. The increase continues up to stage X (5), after which it ceases (Fig. 4, Tab. 2). There is no significant difference in the number of antennal articles between males and females in any stage.

3.2. Reproduction biology and life cycle

Mating behaviour, oviposition and egg development. Mating behaviour and spinning of webs with spermatophores by males, as described by Klingel (1960) and Demange (1956) for the species *L. forficatus* and *L. piceus gracilitarsus* Brölemann, 1898, were not observed for *L. mutabilis* in this investigation.

Of 57 adult females, 26 (both from the field and from laboratory cultures, investigated between 1993 and 1997) laid

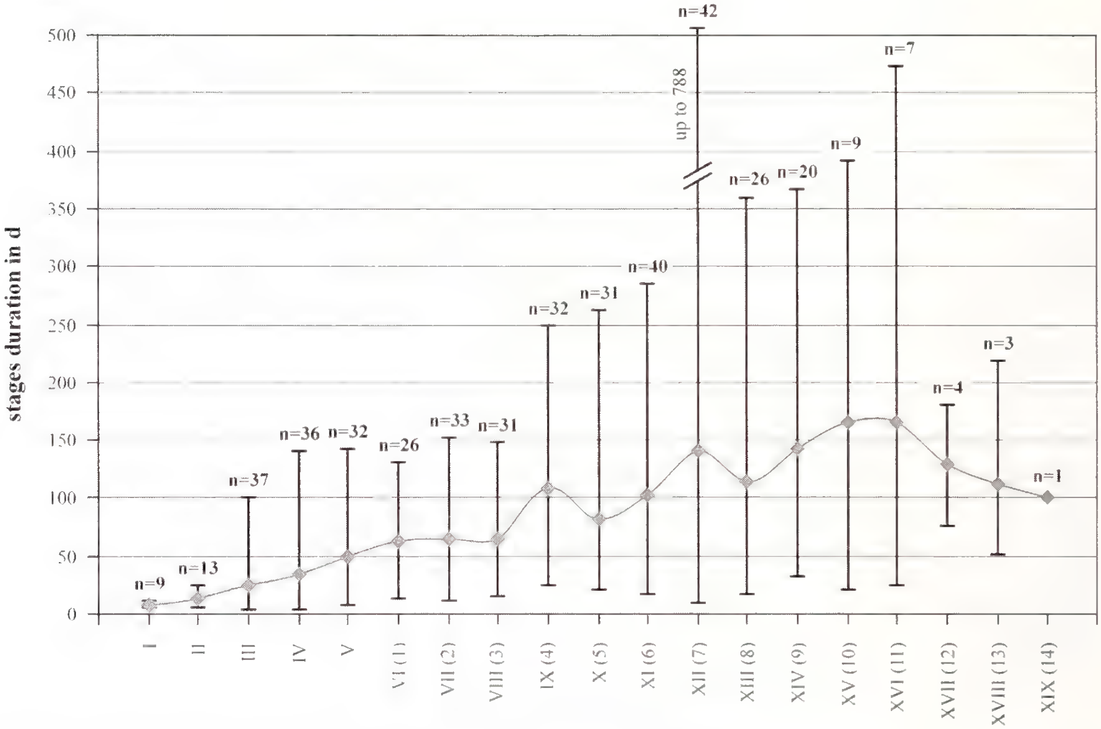

Fig. 5. Average stage duration, minimum and maximum of *L. mutabilis* [in days].

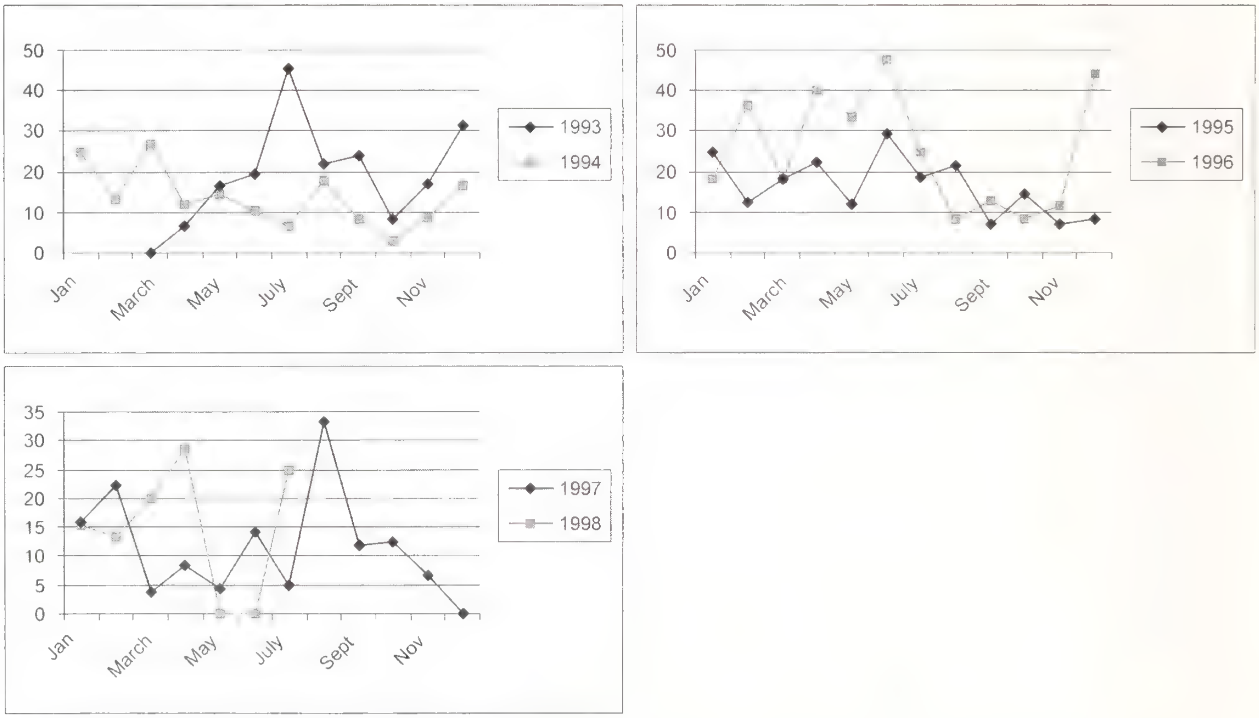

Fig. 6. Moulting activity of *L. mutabilis* in laboratory under constant conditions during the years 1993 to 1998 in % of the total number each month.

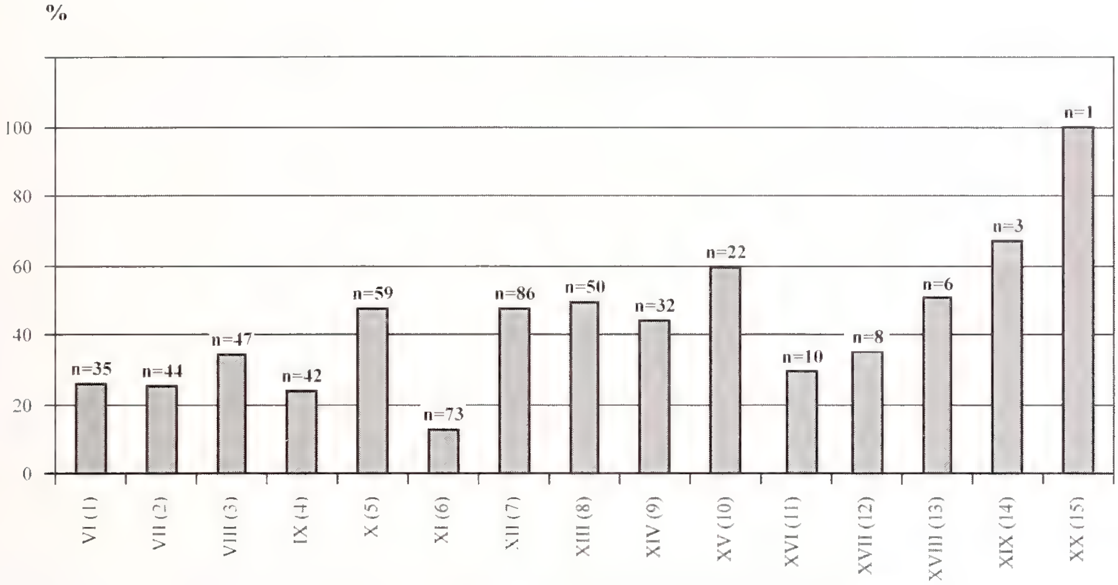

Fig. 7. Mortality rate of epimorphic stages of *L. mutabilis* in % of the total number in these stages.

eggs in captivity, some of them in several successive stages and in several years. Altogether 35 egg laying "periods" were observed by females of stages XI (6) to XVII (12). Egg numbers vary between 1 and 35, on average 11 eggs per female per egg laying period.

The eggs are laid singly. There is no maternal care of the brood in *L. mutabilis* as in other lithobiid species. The only protection for the eggs is a thin cover of fine soil particles, which is applied to the eggs by the female. In the rearing boxes without soil, this behaviour is retained and fine gypsum dust is used by the females. The egg laying itself and the following processes (Brocher 1930 and Serra & Miquel 1996 described it in detail for *L. forficatus* and *L. pilicornis*) could not be observed directly in this study. Only the covered eggs and females carrying eggs with their gonopods could be confirmed.

The eggs of *L. mutabilis*, as in other lithobiid species, are spherical and whitish. The mean diameter is 0.89 mm. The appearance of the youngest stages in nature (Neiße Valley) suggested that oviposition is not connected with a definite time in the year. This was also established by laboratory cultures of *L. mutabilis* in the present study. From 1/3 of laid eggs, young *L. mutabilis* were hatched. Though all eggs were kept under the same constant conditions (16 °C), they needed quite different times for their development. The time between oviposition and hatching ranged between 21 and 284 days (9.5 months). Most individuals hatched after 3-4 months.

Onset of sexual dimorphism and maturity. The sexes of *L. mutabilis* can be distinguished for the first time (with some uncertainty) in stage VII (2), definitely in stage VIII (3). In the laboratory, first egg layings were observed in stage XI (6). Thus XI (6) can be seen as the first mature stage for females.

Duration of stages and moulting activity. The data for the duration of the different stages in the postembryonic development of *L. mutabilis* come from 150 specimens, both laboratory-reared as well as freshly captured. Some 490 moults were observed, 2–11 per individual. Observation of moults every two days was sufficient to ensure accuracy. If moults were not observed directly, at least the remains of exuviae were found. If they were completely eaten by moulted individuals, they could be seen in the faeces.

The mean stage duration increases with stage number (Fig. 5), but with higher variability in older epimorphic stages caused by some "slow" or "fast" individuals. It varies from only a few days to about 500 days. An extreme case was found in stage XII (7). Here, the shortest and longest duration was 10 and 788 days, respectively. The mean duration of stages XVII (12) to XIV (14) is based on only 1–4 animals and is therefore not representative.

However, it was not usual that a specimen had exclusively long (or short) durations of all the stages throughout its life. Therefore, it is possible to make general conclusions about the most important data based upon the average of stage duration (Figs 5, 8). In *L. mutabilis* the first epimorphic stage is reached after 4.5 months and sexual maturity is attained at the earliest after 1.5 years, definitively after 2 years. The maximal life expectancy is about

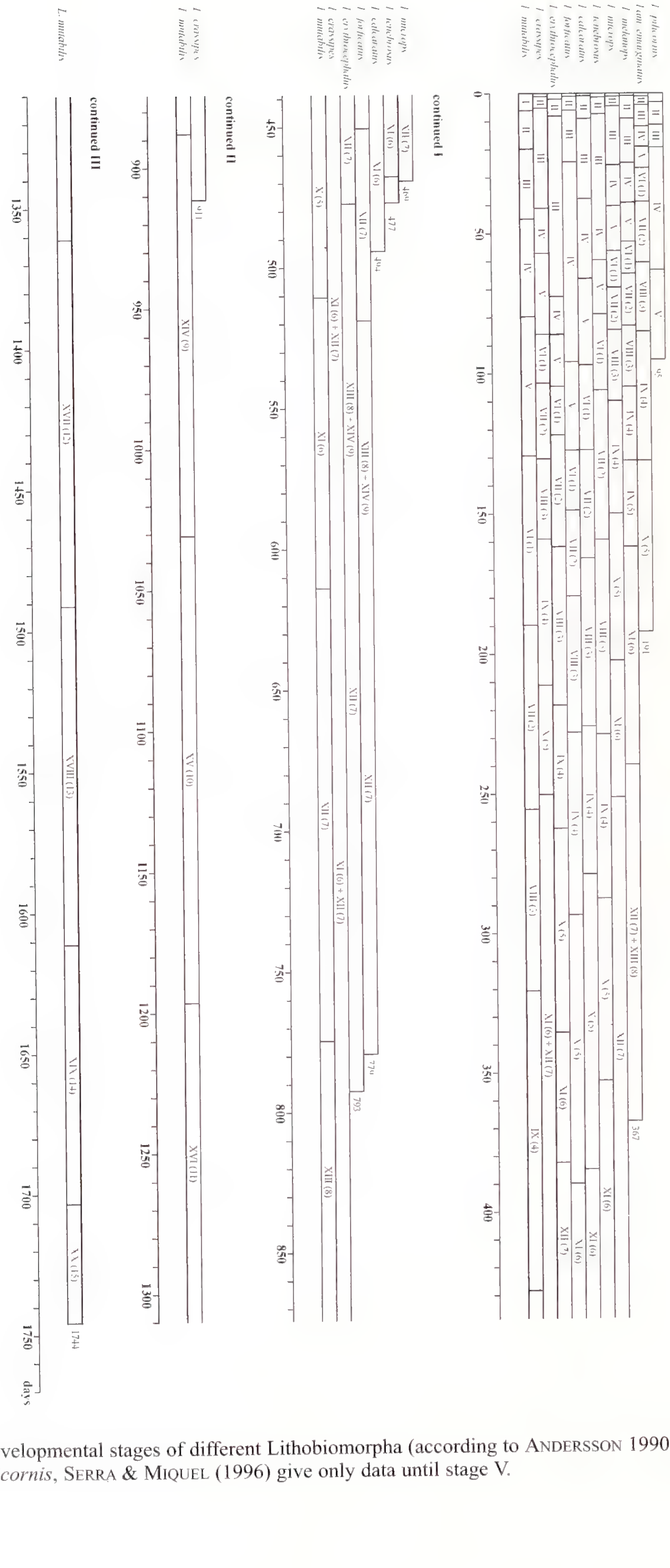

Fig. 8. Duration of developmental stages of different Lithobiomorpha (according to ANDERSSON 1990) and *L. mutabilis* (this investigation). For *L. pilicornis*, SERRA & MIQUEL (1996) give only data until stage V.

5 years. On average, *L. mutabilis* lives 3–3.5 years.

The moulting activity of the epimorphic stages of *L. mutabilis* during the years 1993–1998 can be seen in Figure 6. On average, 27 individuals per month were available. Under constant culture conditions, moults in *L. mutabilis* take place throughout the entire year without any peaks at a specific time.

Mortality. The mortality rate of 213 individuals of the epimorphic stages VI (1) to XX (15) was established. Figure 7 shows the number of dead individuals as a percentage of the total number in these stages. The values are not fully correct, because freshly collected and "laboratory" individuals were analysed together. It is possible that fresh individuals were more viable. Nevertheless, the mortality of the youngest epimorphic stages until XI (4) was very low. The transition from stage X (5) to XI (6), the first mature stage, was only reached by 50% of the individuals. In stage XI (6) the mortality was very low, but then it increased very rapidly. Most of the specimens died in stages XII (7) to XV (10). Only 11 individuals reached stage XVI (11) and only one the highest stage XX (15).

3.3. Observation and discussion on feeding behaviour

Some observations on the feeding behaviour were undertaken in the laboratory. They are compared with results of Pfleiderer-Gruber (1986) and Albert (1983a). These authors studied feeding behaviour more intensively in various centipede species, including *L. mutabilis*, in regard to prey capture, prey spectrum and preference, influence of different food resources on growth, and others.

Animal food. In the laboratory cultures, I offered different animal foods separately to *L. mutabilis* and other species at different time periods. Small pieces of earthworms and living *Tubifex* were given, as well as aphid larvae, small Diptera larvae and also Collembola. The choice of prey depended on the size relationship between predator and prey. Small collembolans (*Folsomia* spec.) were only attacked by juveniles of *L. mutabilis* and smaller species of the subgenera *Monotarsobius* and *Sigibius* [*L. austriacus* (Verhoeff, 1937), *L. microps*]. They noticed the prey only when their antennae came into direct contact with it. The observed feeding process is in correspondence with the description by Rilling (1968).

Minced meat was refused, contrary to results from Pfleiderer-Gruber (1986), who found it to be eagerly taken after 14 days of food withdrawal. Particularly bad results were experienced with ox heart. It led to a mass occurrence of mites (Heterocerconids) in the rearing vessels. Their nymphs attacked the *Lithobius* species so massively, that they could not feed or were unable to move.

Cannibalism. *Lithobius mutabilis* was never observed to feed on members of the same species during the entire investigation period of more than 5 years, provided that the individuals had approximately the same size and were not injured. Once, a *L. forficatus* was observed attacking a defenceless specimen of the same species during moulting. The specimen bit at first in the "neck", fed then on softer interior substances before eating pieces of the integument.

Plant food. In my investigations, I always offered green leaf pieces of indoor plants in addition to other food. In most cases, these plant pieces were clearly nibbled off.

According to Pfleiderer-Gruber (1986), all Chilopoda are pure carnivores and never eat plant material, detritus or soil, in contrast to other literature (e.g. Dobroruka 1961). Pfleiderer-Gruber assumed that such particles, which were only found as gut contents, were accidentally picked up with other food, or it could be still undigested gut contents of herbivorous prey. Albert (1983a) also writes that *L. mutabilis* does not seem to be able to feed on litter, even in times of food shortage.

My investigation refutes these doubts, at least in the case of *L. mutabilis*, which is able to bite off plant parts as food in small amounts. Therefore, it can be assumed that this species also can take in vegetable food under natural conditions.

4. DISCUSSION

4.1. Character analyses

Growth analysis. The growth of body parameters shows sigmoid curves corresponding to the two types of development: after a slow beginning during the first five anamorphic stages, linear growth rises more rapidly after the onset of epimorphic development. Then, stages XIV (9) to XX (15) seem to grow more slowly than the younger stages. However, this may be a result of the low number of individuals studied. An approximately linear growth of the body parameters of epimorphic stages is also found for many other *Lithobius*-species (Albert 1982; Andersson 1976–1984; Kos 1997; Voigtländer 2000). It seems to be typical for all Lithobiomorpha.

In millipedes, maturity often causes a cessation of growth because all reserves are used for the development of eggs and sperm (e.g., Voigtländer 1987, 1996). This could not be established for *L. mutabilis* in the present in-

Table 3. Lithobiomorpha with investigated life cycles (or at least some aspects of it). * = examples for detailed descriptions of immature stages

Taxon	Author(s)
Arenobius manegitus (Chamberlin, 1911)	Chamberlin (1917)*
Bothropolys asperatus (L. Koch, 1878)	Murakami (1958)
Esastigmatobius longitarsis Verhoeff, 1934	Murakami (1960d)
Ethopolys xanti (Wood, 1863)	Chamberlin (1925b)*
Eupolybothrus nudicornis (Gervais, 1837) [Syn. *E. elongatus* (Newport, 1849)]	Daas et al. (1996)
Eupolybothrus grossipes (C.L. Koch, 1847)	Eason (1970)*
Lamyctinus coeculus (Brölemann, 1889)	Andersson (1979, 1990)
Lamyctes emarginatus (Newport, 1844) [Syn. *L. fulvicornis* Meinert, 1868)]	Andersson (1979, 1984b, 1990), Zulka (1991)
Lithobius atkinsoni Bollman, 1887	Chamberlin (1925a)*
Lithobius austriacus (Verhoeff, 1937)	Voigtländer 2000
Lithobius borealis Meinert, 1868	Andersson (1979, 1980a, 1990)
Lithobius b. burzelandicus Verhoeff, 1931	Matic & Stentzer (1978)
Lithobius calcaratus C. L. Koch, 1844	Andersson (1979, 1982a, 1990)
Lithobius canaliculatus Murakami, 1963	Murakami (1963)
Lithobius crassipes L. Koch, 1862	Andersson (1979, 1981, 1990), Wignarajah (1968)
Lithobius curtipes C. L. Koch, 1847	Albert (1982, 1983b), Andersson (1979, 1983, 1990)
Lithobius dentatus C. L. Koch, 1844	Voigtländer 2000
Lithobius erythrocephalus C. L. Koch, 1847	Andersson (1978b, 1979, 1990), Voigtländer (2000)
Lithobius forficatus (Linné, 1758)	Chamberlin (1925a)*, Verhoeff (1925), Brocher (1930), Lewis (1965), Wignarajah (1968), Andersson (1976, 1979, 1990)
Lithobius hirsutipes Eason, 1989	Eason (1989)*
Lithobius lapidicola Meinert, 1872	Andersson (1980a)
Lithobius macilentus L. Koch, 1862	Andersson (1990)
Lithobius melanops Newport, 1845	Andersson (1979, 1980b, 1990)
Lithobius microps Meinert, 1868	Andersson (1979, 1982b, 1990), Voigtländer (2000)
Lithobius mutabilis L. Koch, 1882	Albert (1982, 1983b), Fründ (1983)
Lithobius nihamensis Murakami, 1960	Murakami (1961)
Lithobius obscurus azoreae Eason & Ashmole, 1992	Eason & Ashmole (1992)*
Lithobius pachypedatus Takakuwa, 1938	Murakami (1960a, b, c)
Lithobius peregrinus Latzel, 1880	Barber & Eason (1986)*
Lithobius pilicornis Newport, 1844	Serra & Miquel (1996)
Lithobus schawalleri Eason 1989	Eason (1989)*
Lithobius tenebrosus fennoscandicus Lohmander, 1948	Andersson (1984a, 1990)
Lithobius punctulatus C. L. Koch, 1847 [Syn. *L. validus* Meinert, 1872]	Kos (1997)
Lithobius variegatus Leach, 1814	Roberts (1957), Eason (1964)*, Lewis (1965)
Nothembius insulae Chamberlin, 1916	Chamberlin (1916)*
Oabius pylorus Chamberlin, 1916	Chamberlin (1916)*
Paobius boreus Chamberlin, 1916	Chamberlin (1916)*
Tidabius tivius (Chamberlin, 1909)	Chamberlin (1913)*

vestigation. In spite of the early maturity, at stage XI (6), this species still grows continuously in all measured parameters. Corresponding results were published by Fründ (1983) (head width) and Albert (1982) (body length, head width) for *L. mutabilis*.

Coxal pores. In all Lithobiomorpha, the first coxal porus is developed on the leg 12 in stage V already, whereas the coxal pores of legs 13–15 appear in stage VI (1) at first. The present investigation corroborates this for *L. mutabilis* (Fig. 2). In contrast to other species (e.g., *L. erythrocephalus*, *L. melanops*, *L. crassipes*, *L. curtipes)*, where two pores may be observed on leg 12 of stage VI (1) (Andersson 1978b, 1980b, 1981, 1983), for *L. mutabilis* only one coxal pore was found in all individuals of stage VI (1).

As a general rule for Lithobiomorpha shown in many investigations (Tab. 3), no more than one coxal pore per leg is added during a moult. For this reason, the number of pores of legs 13–15 does not exceed the number of the epimorphic stage; rarely it is the same at least. Only on leg 12, one more coxal pore is possible, because one pore is already developed in stage V. Therefore, the number of coxal pores is a very good character for separating the different stages of *L. mutabilis*, just as in other *Lithobius*-species.

For some species, e.g., *L. calcaratus*, *L. crassipes*, *L. curtipes* (Andersson 1981, 1982a, 1983), *L. piceus* and *L. tricuspis* (Tobias 1969), it was established that coxal pores are more numerous in females than in males. This is also valid for *L. mutabilis*.

Neiße Valley- and Steigerwald-populations show approximately the same numbers of coxal pores summarized from the last four legs in minimum, maximum and "mean" (Tab. 2). The "mean" values differ only by 1–2 (3) pores. The differences between minimum values and maximum values, respectively, are a little higher (up to 7 pores). In both studies, females had significantly more coxal pores than males.

If a comparison between the coxal pores of each leg is made, a very close similarity between the populations can also be seen (Fig. 3 herein and fig. 2 in Fründ 1983). Not only are the numbers of pores on each leg the same in comparable stages, but also the distribution of the numbers. In both studies, legs 13 and 14 reach the most (7) coxal pores. In the present investigation, the number of coxal pores increases to 8 or 9 in later stages, not found by Fründ (1983).

If Albert's (1982) PL1 consists of two different stages, then the number of coxal pores is similar to Fründ's and the studies presented here.

Ocelli. In the investigations at Steigerwald (Fründ 1983), variations in the number of ocelli begin in stage VI (2) (Tab. 2), whereas in the present study they start during anamorphic development in stage IV (Fig. 3). However, in stage VI (1) the usual number was 5, as in the Steigerwald-population. The increase of the number of ocelli was more regular in the investigations by Fründ (1983) than in the presented study, where some successive stages show the same number of ocelli on average.

The increase of ocelli during post-embryonic development of *L. mutabilis* shows more or less the same pattern as in other *Lithobius*-species. With the exception of *L. forficatus, L. variegatus* and *L. pilicornis*, all species investigated up to now have two ocelli in the first three anamorphic stages. Then a more or less linear increase can be observed. However, in higher stages, a greater variability in increase of ocelli number occurs. Differences between the sexes do not exist in all *Lithobius* species, and irregularities between the left and right side are rare.

Antennal articles. In the present investigation, a gradual increase in the mean numbers of antennal articles is only seen until stage X (5). However, in the population from Steigerwald (Fründ 1983) this cessation in increase occurs later [XI (6)]. The numbers reached in the different stages are mostly smaller in the present investigation and some differ very much from those observed by Fründ (1983) (Table 2). The variations within stages are larger, as is the overlap between different stages. Altogether, the growth of antennae in the population from Steigerwald is more regular than in that of the Neiße Valley-population. The numbers of antennal articles of specimens from Solling (Albert 1982) show also high variation, especially in the younger stages (Tab. 2).

In comparison with other Lithobiomorpha (Andersson 1976–1984), there are no differences for the first three anamorphic stages. In later stages of *Lithobius*, the increase takes place in two different ways. In some species (*L. melanops*, *L. calcaratus*, *L. tenebrosus fennoscandius*), the increase continues until the last stage almost in linear fashion. In others (*L. microps*, *L. erythrocephalus*, *L. forficatus*), the growth of antennae is almost completed at a specific stage [IX (4), X (5), XI (6) or XII (7)]. To this group belongs *L. mutabilis* [stagnation from X (5)].

Characteristically for all *Lithobius*-species (including *L. mutabilis*) is the absence of differences in the number of antennal articles between males and females. The extensive variation in the number of antennal articles within a stage in all species is also typical, but may partly result from undetected regeneration. Therefore, the use of this character for stage determination is restricted.

4.2. Number of stages

Like all Lithobiomorpha, *L. mutabilis* develops by hemianamorphosis with five anamorphic and a various number of epimorphic stages. VERHOEFF (1905) described only five epimorphic stages for *L. mutabilis* and called them "status agentilis" (realized by BRÖLEMANN [1930] and JOLY [1966] as "agentilis I" and "agentilis II"), "status immaturus", "status praematurus", "status pseudomatururs" and "status maturus". ALBERT (1982) and FRÜND (1983) distinguish nine epimorphic stages.

How can differences in the number of observed stages come about? ALBERT (1982) and FRÜND (1983) almost exclusively investigated animals that were collected in the field. Only a few individuals were reared for testing in the laboratory. It is impossible to determine the exact epimorphic stage of field animals, because the range of variation of all characters used for stage determination is very large and overlaps between stages. Only direct observation of moulting in the laboratory makes it possible to determine the correct number of stages. Additionally, most individuals die in stages XIII (7) to XV (10), even under favourable conditions in the laboratory (Fig. 6). Thus, it is conceivable that, in the field, death happens even earlier. FRÜND (1983) sampled most individuals at stages X (5) to XII (7). In the Neiße Valley more than half of all sampled individuals were found to be stages XI (6) and XII (7). Later stages were sampled very rarely (20%) in the Neiße Valley.

4.3. Life cycle

Oviposition. Oviposition in *L. mutabilis* is not connected with a certain time of year. This was established by laboratory cultures in the present study as well as by investigations of ALBERT (1979, 1983b). According to LEWIS (1965) and WIGNARAJAH & PHILLIPSON (1977), lithobiids are able to lay eggs during the whole year (*L. variegatus*), but some species (e.g., *L. forficatus*) have a main egg-laying period in spring and a smaller one in autumn. This different behaviour of the species and the small number of eggs laid during each oviposition period might be interpreted in correlation to habitat choice. A long egg-laying period guarantees a breeding success, even if some of the eggs are destroyed through unfavourable conditions, such as dryness. The behaviour of *L. variegatus* (LEWIS 1965) and *L. mutabilis* may indicate that they are less resistant to climatic extremes than *L. forficatus*. Both species live in woodland, whereas *L. forficatus* is more euryoecious and often prefers dry habitats.

A female *L. mutabilis* can lay eggs in several periods (each of these periods can reach up to two months), each separated by one moult at least. In *L. forficatus* – as well as in some diplopods – the development of the eggs and moults is subject to mutual hormonal mechanisms of regulation (RICHTER 1967; SCHEFFEL 1969; LEUBERT & SCHEFFEL 1984; VOIGTLÄNDER 1987). The same mechanisms seem to control the life cycle of *L. mutabilis*.

Egg development. The present investigation shows a large variation in the duration of egg development. This agrees with other studies on *L. mutabilis*. ALBERT (1983b) ascertained individually variable developmental times between 27–269 days (15 °C) and TUF (2002) found time periods of approximately 150-200 days under natural conditions.

This different "hatching period" in combination with a long egg-laying period characterises the life strategy of *Lithobius* in general, not only of *L. mutabilis*. It guarantees the survival of at least some individuals.

Onset of maturity and insemination time(s). In agreement with the present results, ALBERT (1983b) also defined stage XI (6) as first mature stage of *L. mutabilis*. FRÜND (1983) deduced from investigations of the structure of the secondary sex characters that X (5) is not yet adult, but stages XII (7) to XIV (9) definitely are.

To determine the first stage of maturity in males, it is necessary to examine the testes, i.e. whether they contain sperm. It is not possible to prove this in breeding cultures. Each female was kept with one or two males, but it is not certain whether their eggs were fertilized by the males present, because females are able to conserve sperm in their seminal receptacles for up to two years (personal observations on a lone female). The same phenomenon was found in Scutigeromorpha (MURAKAMI 1956, DOHLE 1969). TOBIAS (1969) observed egg laying in *Lithobius* seven months after isolation of the females and VERHOEFF (1915) after approximately one year. Personal observations support the period of one year for *L. forficatus*.

Individual development. The high individual variability of stage duration (Fig. 5) means that new developmental periods (epimorphic development, maturity) begin at very different times in each individual. Moulting activity and stage duration depend to a large degree on the environmental conditions. Mostly food shortage and low temperatures inhibit development (ROBERTS 1957; JOLY 1977; ANDERSSON 1978a). The loss of extremities can stimulate moulting (VERHOEFF 1915; SCHEFFEL 1980).

Under constant temperature conditions and optimal feeding in the present study, it was expected that all individuals would have a relatively similar stage duration. But, on the contrary, they varied very widely especially in higher epimorphic stages. This is not only a phenomenon of

L. mutabilis, but occurs in other species too (ANDERSSON 1990).

However, the individual differences in stage duration in the studies of ANDERSSON, ALBERT, and myself cannot be caused by hunger, since all individuals were well fed in all investigations. Further, the different constant culture temperatures (ANDERSSON: 20 °C, ALBERT: 15 °C, present study: 16 °C) could have had an influence. But ANDERSSON investigated all species under the same conditions and also found large differences between the species additionally to the individual differences. Thus, it seems that environmental conditions have only a secondary influence on intra- and interspecific variability of life span.

To explain the interspecific differences ANDERSSON (1990) suggested the possibility of a "built-in clock" by inspection of moults in different months. The smaller (*Sigibius Monotarsobius*) species, *L. microps* and *L. crassipes*, show many fewer moults during the winter. The larger (*Lithobius* s.str.) species, *L. forficatus* and *L. erythrocephalus*, show no regular differences. Up to now, there is no explanation for the difference in moulting pattern between large and small species. The investigations have shown that *L. mutabilis* moults throughout the entire year under constant temperature conditions. It can thus be assumed that *L. mutabilis* does not have a "built-in clock". This corresponds with the other larger *Lithobius*-species (ANDERSSON 1990).

Population development. The most important life history data for *L. mutabilis* from Neiße Valley are in concordance with those found for the Solling-populations by ALBERT (1983b). The author gave 0.5–1 year till attainment of stage VI (1) (4.5 months in the present paper). Maturity is reached earliest in stage X (5) after 1.5–2 years according to both investigations. The total life span in *L. mutabilis* is suggested by ALBERT's abundances data to be between 4 and 7 years, which is a little longer than in the present study by laboratory observations (3–5 years).

Figure 8 shows the developmental time of different species (according to ANDERSSON 1990; SERRA & MIQUEL 1996) in comparison to *L. mutabilis* (present paper). The shortest stage of *L. mutabilis* was stage I with only 5 to 12 days, which is much longer than in all other investigated species. The first epimorphic stage was reached after 4 months, approximately the same time as in *L. forficatus*, but longer than in other species. *L. mutabilis* has reached stage XI (6) after 510 days only, whereas other species reach this stage as early as after 255–390 days (Fig. 8). This means a very retarded development of *L. mutabilis*. This species has the highest number of stages as well as the greatest age of all species investigated in the laboratory. However, it seems that *L. mutabilis* dies earlier in the field than in captivity.

4.4. Conclusions

The results of the character analyses (growth, biomass, number of coxal pores, antennal articles and ocelli) in the geographically widely separated populations of *L. mutabilis* Steigerwald, Solling (western Germany) and Neiße Valley (eastern Germany) show very high correspondence. The number of stages recognised in this laboratory study was much higher than in the other investigations, perhaps due to methodological problems of stage analyses on older field-collected individuals. However, the life cycles of the different populations are very similar. This suggests that in *L. mutabilis* the study of an isolated case can be generalised and this may also be true for other species.

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Amphibians and Reptiles of the Tchabal Mbabo Mountains, Adamaoua Plateau, Cameroon

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Abstract. Tchabal Mbabo is a remote mountain range in Central Cameroon which covers 79,000 ha; only three amphibian and no reptile species are listed for this area. We conducted two expeditions, in 1998 and 2000, to survey the herpetofauna. We used opportunistic visual encounter surveys and driftfence/pitfall trap arrays for sampling. Our findings increased the number of amphibian and reptile species known for the area to 15 each. We discovered one recently described new frog species (*Cardioglossa alsco*) and found an additional six species of anurans and one lizard species which could not be assigned to any described species. The deceptive endemism of amphibians for this area is remarkable. We report a range extension of 400 km and montane gallery forest as a novel habitat for the skink *Lacertaspis chriswildi*. The importance of the montane forests on the northern slopes as well as the gallery forests on the southern slopes of the mountain range are highlighted.

Keywords. Amphibia, Reptilia, Tchabal Mbabo Mtns, Adamaoua Plateau, Cameroon, faunistics, conservation.

1. INTRODUCTION

Although herpetological work in Cameroon has been recurrent during the last half century (PERRET 1959, 1960, 1961, 1966; AMIET 1971; BÖHME 1975; AMIET 1978; JOGER 1982; BÖHME & SCHNEIDER 1987; EUSKIRCHEN et al. 1999, 2000; LeBreton 1999; SCHMITZ et al. 1999, 2000; HERRMANN et al. 2000, 2005a, 2005b) large areas remain unsampled. Such an area is the Tchabal Mbabo Mtn range on the western border of the Adamoua Plateau (Fig. 1). The Tchabal Mbabo Mtns represent the last segment in the chain of mountains known as "Dorsale Camerounaise", which extends northeasterly from the island of Bioko continuing inland with Mt. Cameroon, Mt. Kupe, the Manengouba Mtns, Mt. Lefo and Mt. Oku.

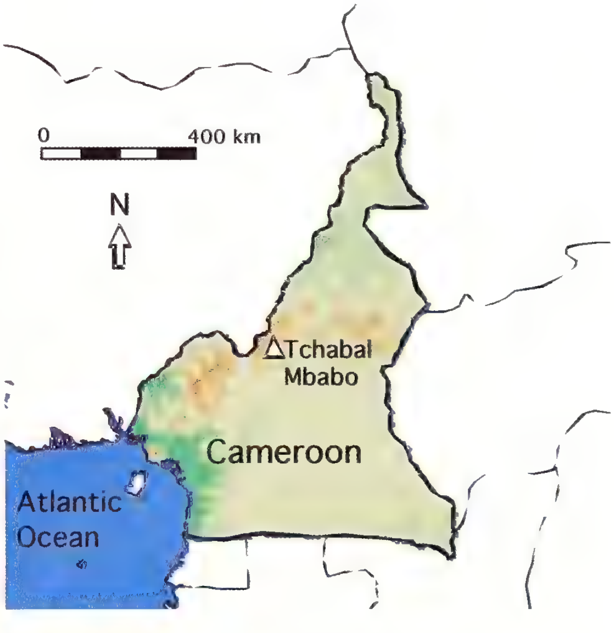

Fig. 1. Location of the Tchabal Mbabo Mtns within Cameroon.

Tchabal Mbabo is a broad horseshoe-shaped mountain massif with a west-eastern orientation and altitudes of up to 2,400 m. Below 1,600 m the massif is connected to other mountains. The area above 1,600 m covers 79,000 ha with 4,900 ha of relict montane forest along the steep northern slopes (Fig. 2a and 2b) adjacent to the rim which represents the northernmost occurrence of this forest type in Cameroon (THOMAS & THOMAS 1996). The southern slopes are extensive grasslands with interspersed gallery

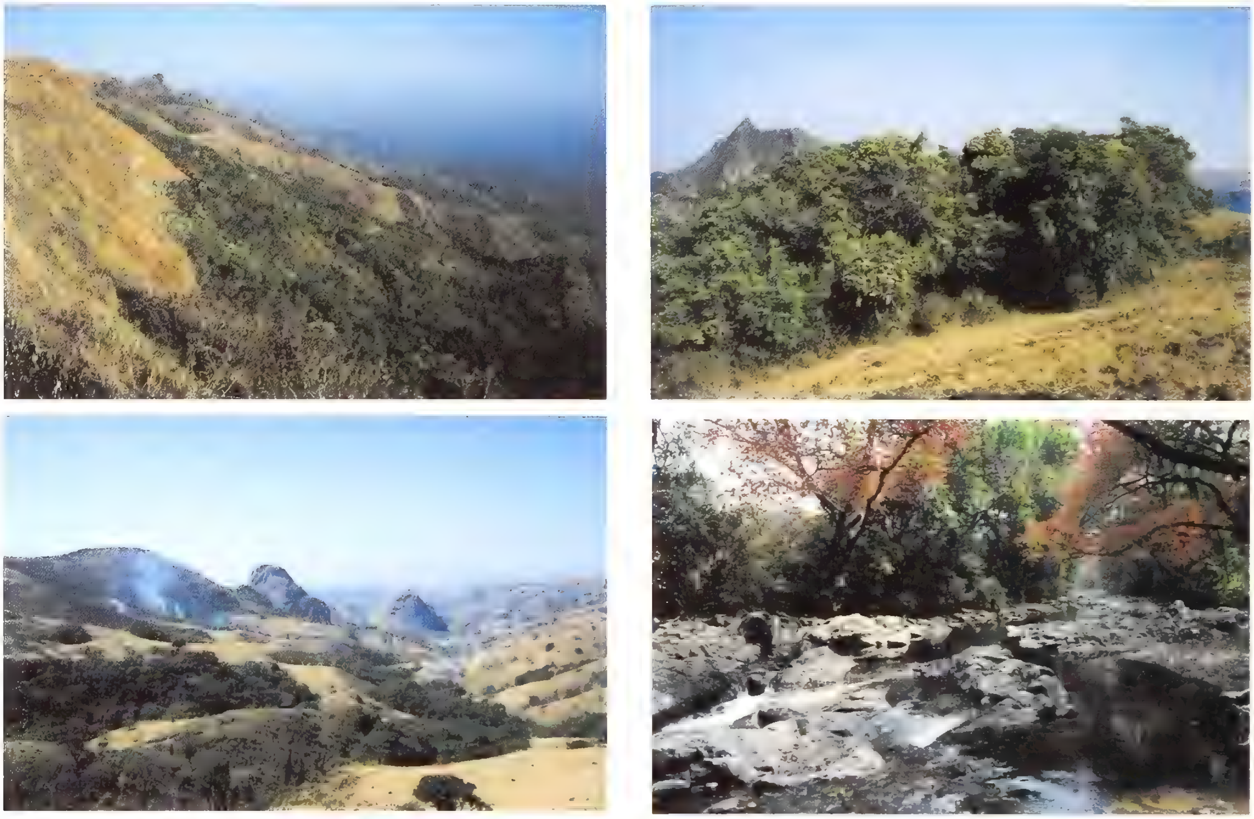

Fig. 2. Different Tchabal Mbabo habitats: (a) northern slope near Fungoi with patches of cloud forest (ca. 2,000m elevation), (b) cloud forest along the rim (ca. 2,000 m elevation), (c) savanna and gallery forest on the southern slopes between Fungoi and Pinku peak (ca. 2,100 m elevation), (d) dry forest along Mayo Selbe (ca. 800 m elevation).

forests along creeks (Fig. 2c). The grasslands are managed by Fulani cattle herdsmen and burned every year. Yearly precipitation at the southern base of the mountains is approximately 1,700 mm (THOMAS & THOMAS 1996). The dry season extends from November to February, precipitation measures < 50 mm/month; the peak rainy season extends from June to October with precipitation up to 300 mm/month. The hottest months are April and May with average daily temperatures of up to 30 °C. Annual temperatures on the plateau average 18 °C with a daily amplitude of 13–15 °C (THOMAS & THOMAS 1996).

We mounted data loggers on tree trunks (two meters height) in forests in the vicinity of Fungoi, at an elevation of circa 2,100 m, which recorded air temperature and relative humidity at one hour intervals. The climatic data for a gallery forest on the south flank is presented in Figure 3. During a data collecting period of 906 days comprising February 2000 to July 2002, the temperature ranged from 8.6 to 26.7 °C ($x = 15.4$ °C). The relative humidity ranged from 13 to 100 % ($x = 81$ %). Data was also collected on the north flank of the mountain at an elevation of circa 2,100 m from February 2000 to May 2001 over a period of 465 days. Here the temperature ranged from 10.2 to 34.9 °C ($\bar{x} = 16.2$ °C) and the relative humidity ranged from <5 to 100 % ($\bar{x} = 65$ %). These data indicate the northern slope to be considerably warmer and drier.

The presence of a well developed montane forest ecosystem of the rare northern type and the geographical isolation of the area have led to a number of hypotheses postulating undescribed herpetological species, especially in the montane forest patches of the Tchabal Mbabo (BÖHME & KLAVER 1981; BÖHME & SCHNEIDER 1987).

Jean-Louis AMIET (Nyons, pers. comm. 2003) surveyed the area around Hama Aoudi in May 1970 and December 1972. In 1978, Amiet lists an undescribed species of *Bufo* (*B.* sp. 2, "espèce orophile du Tchabal Mbabo") and an undescribed species of *Phrynobatrachus* (*P.* sp. 5, "espèce orophile endémique du Tchabal Mbabo") in his "Liste provisoire des amphibiens anoures du Cameroun". THOMAS & THOMAS (1996) report on a forthcoming herpetologi-

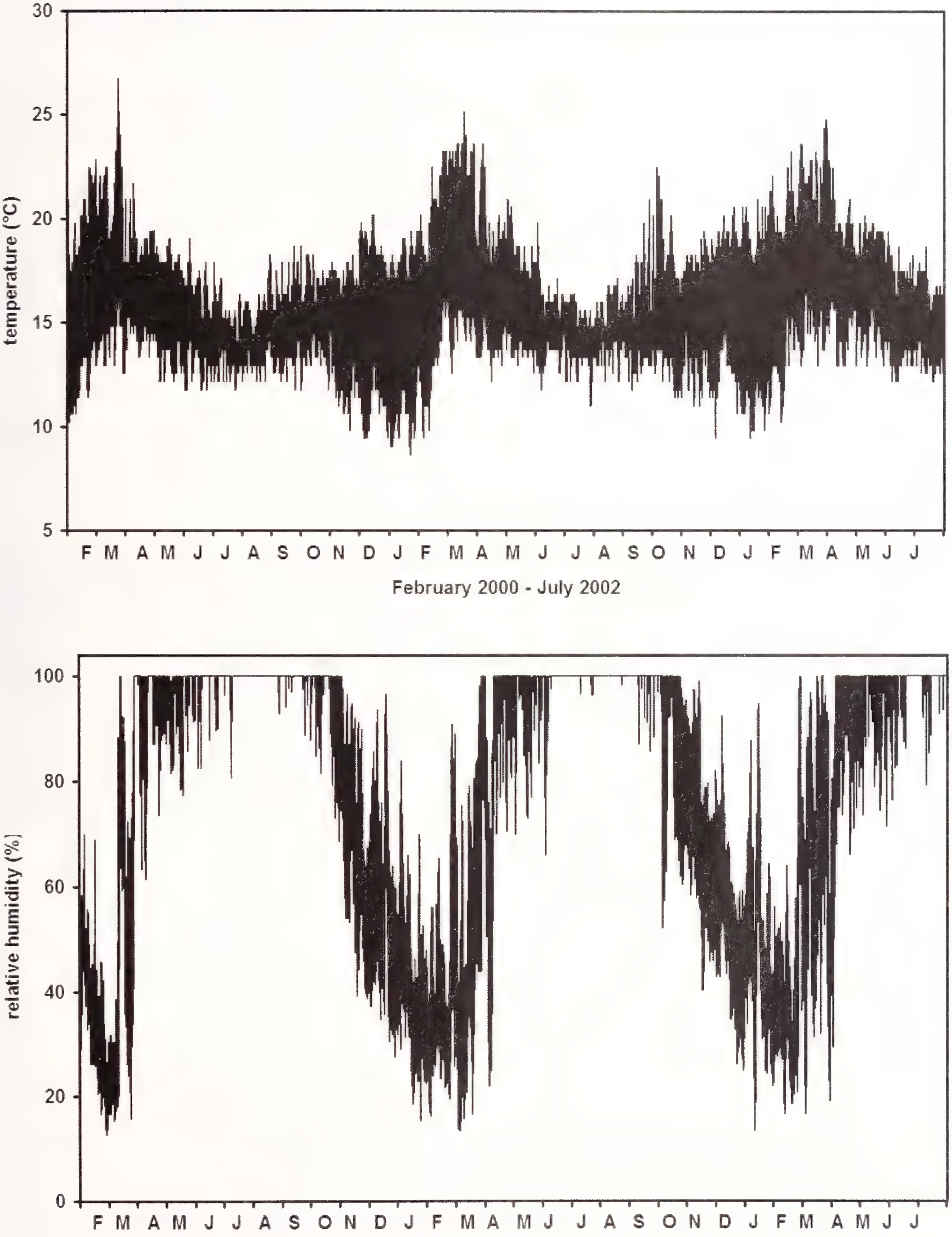

Fig. 3. Temperature in °C (a) and relative humidity in % (b) over a period of 30 months in a gallery forest in the vicinity of Fungoi on the south flank of Tchabal Mabao at an elevation of approximately 2,100 m.

cal survey by Dwight Lawson, who apparently visited the area in August 1997 (LAWSON 2000). In the literature very few amphibians and reptiles have been reported from Tchabal Mbabo: *Astylosternus rheophilus tchabalensis* Amiet, 1977, *Leptopelis nordequatorialis* Perret, 1966 (in BÖHME & SCHNEIDER 1987) and *Crotaphatrema tchabalmbaboensis* Lawson, 2000 (see LAWSON 2000).

In January / February 2000 we (H.-W.H., A.S. & P.A.H.) surveyed the herpetofauna of Tchabal Mbabo for 14 days. This period is at the end of the dry season and was chosen by need of vehicle accessibility. Accordingly, we experienced no rain which may have influenced the number of species found. Additionally, in November 1998 a two week herpetological sampling expedition was conducted by two native field assistants at the beginning of the dry season. Here we present a systematic list of the combined findings of these two expeditions.

2. RESULTS

2.1. Survey sites

We surveyed the following localities (vegetation characterization follows LETOUZEY 1968 and THOMAS & THOMAS 1996). Altitude was measured with a Global Positioning System (GPS) unit and verified with a conventional altimeter.

1. Sambolabo, 7°04'94"N, 11°59'06"E, 1,032 m elevation, southern slope, Sudano-guinecan savanna with *Daniellia oliveri* and *Lophira lanceolata*, very degraded and managed as permanent pasture.

2. Mayo Kelele, 7°10'78"N, 12°01'68"E, 1,675 m elevation, southern slope, submontane wooded *Hyparrhenia* savanna, gallery forests with *Syzygium guineense*.

3. 5 km NEE of Fungoi, 7°15'11"N, 12°03'58"E, 2,060 m elevation, on crest of southern slope, montane grassland with *Sporobolus indicus* and gallery forest dominated by *Syzygium guineense*, *Ilex mitis* and *Symphonia globulifera*, northern slope with montane forest and scrub.

4. Hunter's Hut, 7°18'81"N, 12°02'83"E, 1,282 m elevation, northern slope, savanna with *Lophira alata* and *Daniella oliveri*, gallery forest diverse with many semi-deciduous species.

5. Mayo Selbe (Fig. 2d), 7°21'88"N, 12°02'58"E, 790 m elevation, for landscape and vegetation see Hunter's Hut.

6. Dodeo, 7°28'03"N, 12°04'10"E, 681 m elevation, savanna with *Isoberlinia doka*, including gallery forests along flat flood plains, often with wetland prairies.

7. Sanganadje, no coordinate data, 1,000 m elevation, ca. 15 km SSE of Galim, for landscape and vegetation see Hunter's Hut.

2.2. Survey methods

Opportunistic visual encounter surveys (CRUMP & SCOTT 1994) were the predominant survey method we used. We sampled during day and night time. Additionally we installed three Y-shaped drift fence/pitfall trap arrays with 5 m long segments (CORN 1994) in the vicinity of study site 3 near Fungoi. Two arrays were situated in a gallery forest (southern slope), one close to a creek. The third array was on a steep slope in the montane forest of the northern slope of the ridge. We worked the drift fences for the full study period of two weeks in January / February 2000, with two controls of pit falls every day (morning and evening), without trapping success.

2.3. Species account

Nomenclature in the subsequent systematic list of amphibian and reptile species follows FROST (2002) for amphibians and UETZ et al. (2004) for reptiles. All voucher specimens are deposited in the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK) or in the collection of the senior author (HWH) in Cameroon. The latter specimens will be transferred to the herpetological collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Anura
Bufonidae

Bufo maculatus Hallowell, 1854
Locality: 10 km E of Sambolabo, in village, 1 specimen, ZFMK 68945 (15.XI.–7.XII.1998).

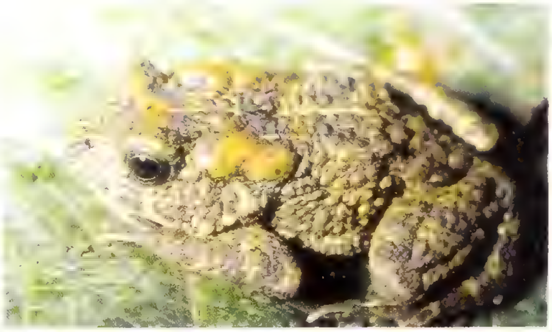

Fig. 4. *Bufo* sp. (cf. *Bufo* sp. 2 sensu AMIET, 1978).

Bufo regularis Reuss, 1834
Localities: Sambolabo, in village, 2 specimens, ZFMK 75630 (`, 24.I.2000), ZFMK 75730 (7.II.2000); Dodeo, in village, 1 specimen, ZFMK 75631 (´, 2.II.2000).

Bufo sp. (cf. *Bufo* sp. 2 sensu AMIET 1978) (Fig. 4)
Locality: 5 km NEE of Fungoi, in creek in gallery forest on southern slope, 1 specimen, ZFMK 75769 (subadult, 30.I.2000).
Remarks: The specimen possesses smooth paratoid glands which are medially constricted.

Arthroleptidae
Arthroleptinae

Arthroleptis sp. (Fig. 5)
Locality: Hunter's Hut, near small creek in gallery forest, 1 specimen, ZFMK 75704 (31.I.2000).

Cardioglossa alsco Herrmann, Herrmann, Schmitz & Böhme, 2004 (HERRMANN et al. 2004)
Locality: 5 km NEE of Fungoi, in creek in gallery forest on southern slope, 73 specimens, ZFMK 75713-25, 77677-736 (11 ♂, 13 ♀, 49 subadults, 28.–29.I.2000).

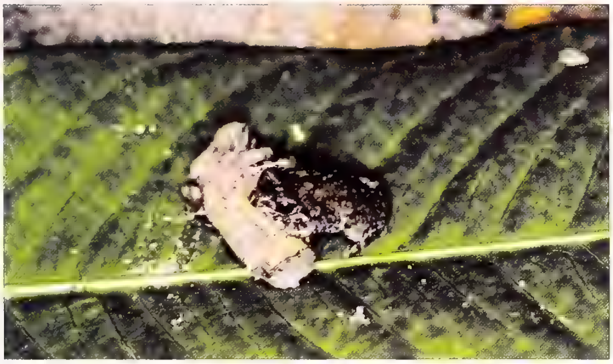

Fig. 5. *Arthroleptis* sp. from small creek on northern slope at ca. 1,200 m elevation.

Astylosterninae

Astylosternus Werner, 1898
Remarks: All *Astylosternus* were strongly polymorphic and difficult to assign to any described taxon. We identified *A. rheophilus tchabalensis* based on morphology. Based on a 600 bp long segment of the 16S rRNA gene we identified two of the other polymorphic *Astylosternus* as conspecific with the latter species.

Astylosternus rheophilus tchabalensis AMIET, 1977
Locality: 5 km NEE of Fungoi, in creek in gallery forest on southern slope, 5 specimens, ZFMK 75770-4 (30.I.–5.II.2000).
Remarks: Our specimens show a remarkable polymorphism and differ from topotypic *A. r. rheophilus* of Mt Lefo (Fig. 6a and 6b).

Astylosternus sp. (Fig. 6c and 6d)
Locality: Mayo Selbe, in creek in gallery forest, 4 specimens, ZFMK 75775-8 (2./3.II.2000).

Astylosternus sp. indet.
Locality: Dodeo, in creek in gallery forest, 15 tadpoles, ZFMK 75632-42 (5.II.2000).

Leptodactylodon sp.
Locality: 5 km NEE of Fungoi, in creek in gallery forest on southern slope, 1 juvenile specimen, ZFMK 75703 (4.II.2000).

Ranidae
Raninae

Amnirana longipes (Perret, 1960)
Locality: Sanganadje, 2 specimens, ZFMK 68946-7 (15.XI.–7.XII.1998).

Ptychadena sp.
Locality: Sanganadje, 1 specimen, ZFMK 68948 (15.XI.–7.XII.1998).

Phrynobatrachus steindachneri Nieden, 1910 (Fig. 7a)
Locality: 5 km NEE of Fungoi, in creek in gallery forest on southern slope, 8 specimens, ZFMK 75705-12 (28.I.2000).

Phrynobatrachus spp. (Fig. 7b)
Locality: 5 km NEE of Fungoi, in creek in gallery forest on southern slope, 64 specimens, ZFMK 75643-702, 75726-9 (28.I./4.II.2000).
Remarks: Juvenile to subadult specimens with some probably being *P. steindachneri*. Others could not be identified.

Hyperoliidae

Hyperolius riggenbachi Nieden, 1910
Locality: Sanganadje, 8 specimens, ZFMK 68949-56 (5 ♂, 3 ♀, 15.XI.–7.XII.1998).

Squamata
Gekkonidae

Hemidactylus brooki Gray, 1845
Locality: Dodeo, 1 specimen, ZFMK 75749 (♀, 2.II.2000).

Agamidae

Agama agama (Linnaeus, 1758)
Localities: Sambolabo, 4 specimens, ZFMK 75731-34 (2 ♂, 2 ♀, 7.II.2000); Mayo Kelele, 4 specimens, ZFMK 75736-39 (2 ♂, 2 ♀, 7.II.2000).

Agama doriae benuensis Monard, 1951
Locality: Dodeo, 1 specimen, ZFMK 75748 (♀, 2.II.2000).

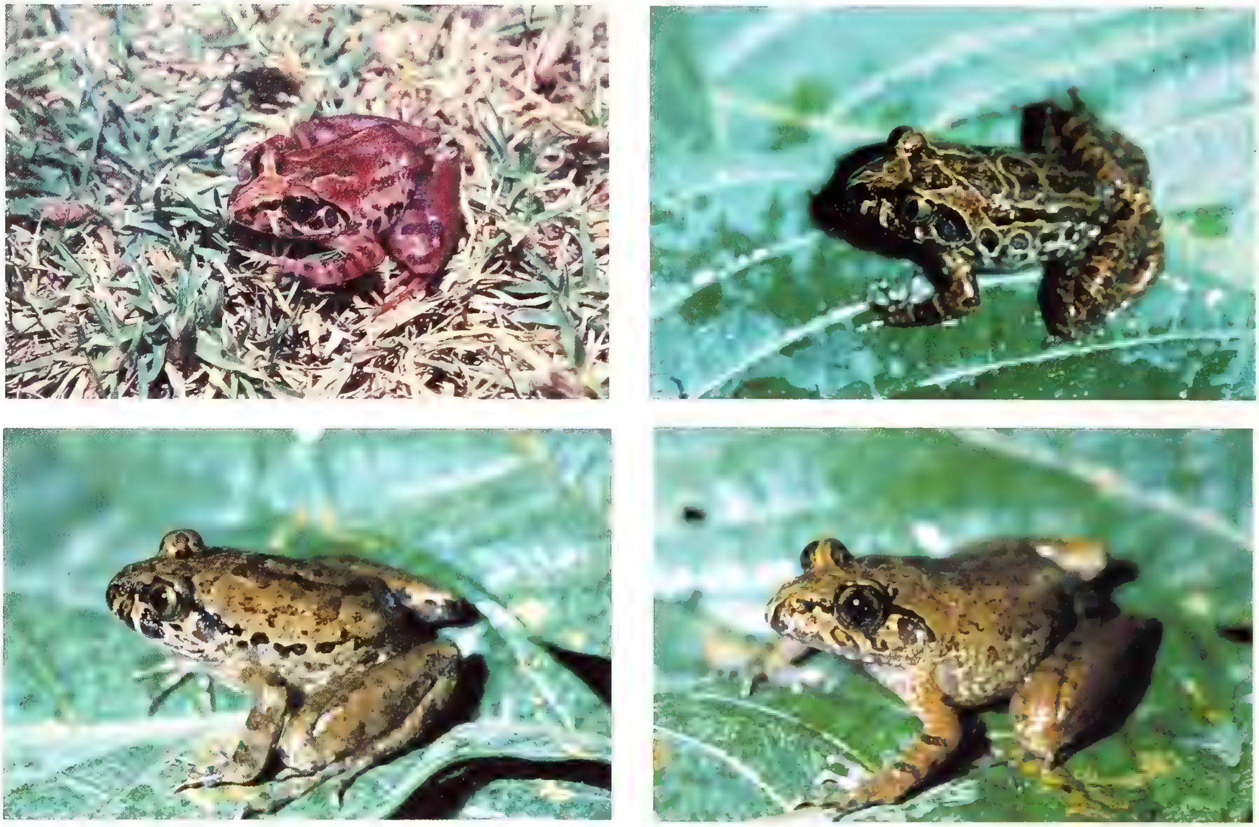

Fig. 6. (a) *Astylosternus rheophilus rheophilus* from Mt Lefo, (b) *Astylosternus* cf. *rheophilus* tchabalensis from near Fungoi at an elevation of ca, 2,000 m, (c) and (d) *Astylosternus* sp. from Mayo Selbe at ca. 800 m elevation.

Chamaeleonidae

Chamaeleo gracilis gracilis Hallowell, 1842
Locality: 15 km E of Sambolabo, 1 specimen, ZFMK 68942 (♀, 15.XI.–7.XII.1998).

Chamaeleo senegalensis Daudin, 1802
Locality: Dodeo, 2 specimens, ZFMK 73092, 75747 (2 ♀, 2.II.2000), Mayo Kelele, 1 specimen, HWH 1214 (♀, no date).

Chamaeleo wiedersheimi wiedersheimi Nieden, 1910
Localities: Mayo Kelele, 1 specimen, ZFMK 68943 (♂, 15.XI.–7.XII.1998), 4 specimens, ZFMK 75740-43 (3 `, 1 ♀, 7.II.2000), 4 specimens, HWH 1210-13 (3 ♂, 1 ♀, no date); 5 km NEE of Fungoi, in gallery forest on southern slope, 3 specimens, ZFMK 75744-46 (1 ♂, 2 ♀, 25.I.2000).

Scincidae

Lacertaspis chriswildi (Böhme & Schmitz, 1996)
Locality: 5 km NEE of Fungoi, in gallery forest on southern slope, 1 specimen, ZFMK 75735 (29.I.2000).

Trachylepis sp.
Locality: 3 km NEE of Mayo Kelele, on path in grassland, 1 juvenile specimen (25.I.2000, Fig. 8).

Remarks: This specimen persisted only as photograph and tissue voucher. We follow Mausfeld et al. (2002) but prefer to use the genus name *Trachylepis* instead of *Euprepis* (sensu Bauer 2003). This specimen resembles juvenile *T. perrotetii* (Duméril & Bibron, 1839) but has a blue tail and shows a clear genetic differentiation from the latter species (Mausfeld-Lafdhiya et al. 2004). A blue tail in juveniles is otherwise only known in *T. quinquetaeniata* (Lichtenstein, 1823) which, however, has a distinctly striped body.

Varanidae

Varanus niloticus (Linnaeus, 1758)
Locality: Sambolabo, 1 specimen (head and skin), ZFMK 68930 (15.XI.–7.XII.1998).

Boidae

Python sebae (Gmelin, 1789)
Locality: Mayo Kelele, 1 specimen (Fig. 9, no date), head of a specimen caught by villagers.

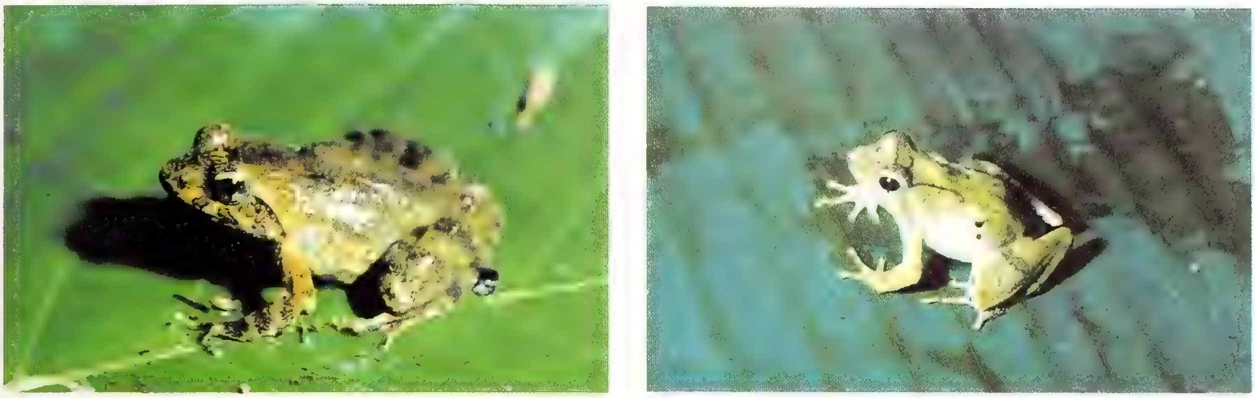

Fig. 7. (a) *Phrynobatrachus* cf. *steindachneri* from gallery forest near Fungoi at an elevation of ca. 2,000 m, (b) *P.* sp. from the same locality.

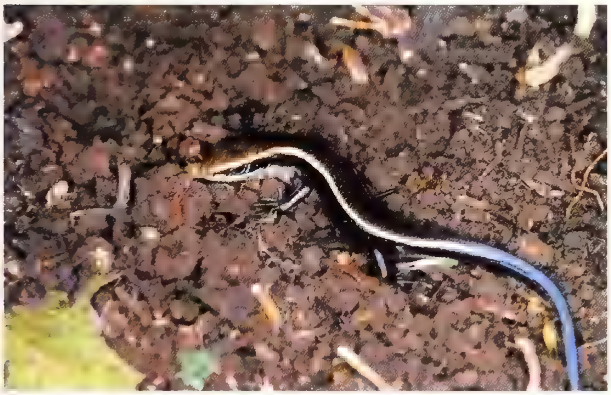

Fig. 8. Juvenile *Trachylepis* sp. from Mayo Kelele.

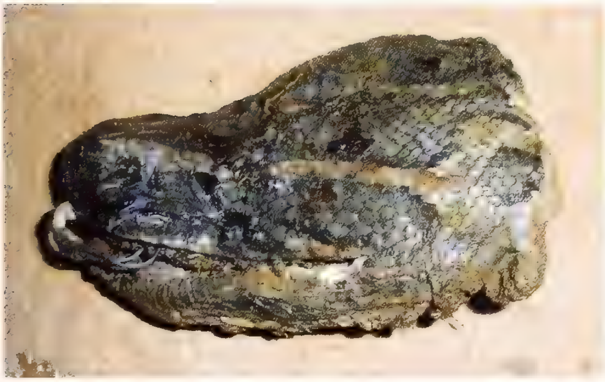

Fig. 9. Head of adult *Python sebae* from hunters at Mayo Kelele.

Colubridae

Philothamnus angolensis Bocage, 1882
Localities: Sangandje, 11 specimens, ZFMK 68931-41 (15.XI.–7.XII.1998); Mayo Kelele, 1 specimen (head), HWH 1218 (no date); 5 km NEE of Fungoi, in gallery forest on southern slope, 1 specimen, ZFMK 75751 (subadult, 2.II.2000).

Elapidae

Dendroaspis jamesoni jamesoni (Traill, 1843)
Locality: Dodeo, 1 specimen, ZFMK 75750 (subadult, 2.II.2000).

Naja nigricollis Reinhardt, 1843
Locality: Mayo Kelele, 1 specimen (head), HWH 1219 (no date).

Viperidae

Bitis arietans (Merrem, 1820)
Locality: 10 km E of Sambolabo, 1 specimen (head), ZFMK 68944 (15.XI.–7.XII.1998).

Causus rhombeatus (Lichtenstein, 1823)
Locality: Mayo Kelele, 3 specimens (heads), HWH 1215-17 (no date).

3. DISCUSSION

A total of 30 herpetological species (one caecilian, 14 anurans, nine lizard and six snake species) are recorded from the Tchabal Mbabo Mtns. The number of recorded amphibian species corresponds with comparable surveys in Western and Central Africa as listed in Rödel & Agyei (2003). However, numbers from thoroughly surveyed savanna/forest areas in West Africa suggest amphibian species counts of at least twice of those presented here.

All species, except *Lacertaspis chriswildi*, are known as either savanna or farmbush/forest edge species and are not restricted to forests. *Astylosternus*, *Cardioglossa* or *Lep-*

todactylodon are predominately found in forests with exception of those species adapted to high elevation grasslands and gallery forests.

Lacertaspis chriswildi is known from only two specimens, the holotype which originated from the high elevation montane forest at Mt Kupe (BÖHME & SCHMITZ 1996) and one further specimen from the Takamanda lowland rainforest, both in Southwestern Cameroon. Our finding represents the first record of this species from a gallery forest within high elevation grassland. It also extends the range of the species approximately 400 km to the northeast. This suggests its occurrence in other areas along the "Dorsale Camerounaise".

The high number of taxa which could not be assigned to any described species (i.e., *Bufo* sp., *Arthroleptis* sp., *Astylosternus* sp., *Leptodactylodon* sp., *Ptychadena* sp. and *Phrynobatrachus* spp.) as well as the discovery of *Astylosternus rheophilus tchabalensis*, *Crotaphatrema tchabalmbaboensis* (LAWSON, 2000) and *Cardioglossa alsco* (HERRMANN et al. 2004) are indicative of both the paucity of knowledge on the Tchabal Mbabo herpetofauna in general and the uniqueness of the anuran fauna with its endemism in particular.

Future surveys to the Tchabal Mbabo Mtns are warranted in order to clarify the taxonomic status of specimens collected during our surveys and to gain comprehension on the extant herpetofauna. The discovery of hitherto undescribed species is likely. Due to the area's remoteness and to the traditional lifestyle of the Fulani herdsmen, no immediate threat to the herpetofauna of the area was observed. Nonetheless, efforts to preserve the unique montane forests on the northern slopes as well as the semi-deciduous and gallery forests are warranted to ensure their welfare in the future. The montane forests on the north-facing slopes are relatively secure due to their extreme topography. The gallery forests on the southern slopes however, are accessible to the Fulani cattle and are increasingly degraded by husbandry practices.

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The Position of *Trochiliphagus* Carriker within the Ricinidae (Insecta: Phthiraptera)

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Abstract. Two forms of the Ricinidae (Mallophaga, Phthiraptera) that live on Trochilidae have independently developed piercing mouthparts. The one (*Trochiloecetes*) is obviously an ancient inhabitant of hummingbirds, whereas the other has settled these birds rather recently. Carriker (1960) established a new genus "*Trochiliphagus*" for the second one. It is demonstrated that these lice belong to *Ricinus* de Geer, 1778, a genus with normal biting mouthparts which is widespread on Passeriformes. *Trochiliphagus* Carriker, 1960 is placed as a junior synonym of *Ricinus* and all species described till now should be named *Ricinus jimenezi*. Within *Ricinus* these hummingbird-dwelling lice are best placed in the *dolichocephalus* species-group. Obviously mouthparts have a high plasticity and are not good for diagnostic characters.

Keywords. *Ricinus jimenezi*, piercing mouthparts, secondary settlement.

1. INTRODUCTION

Clay (1949) detected that among lice with biting mouthparts (= Mallophaga) the members of the genus *Trochiloecetes* Paine & Mann, 1913 that live on hummingbirds have developed piercing mouthparts independent of the Anoplura. She described details of the mouthparts that emerged from the hypopharynx and the ligular sclerites. According to Clay the mandibles are reduced.

Rather incidentally Clay mentions that on hummingbirds there are also members of the genus *Ricinus* de Geer, 1778 that have also lost the typical mouthparts of Mallophaga, though the changes are not as far-reaching as in *Trochiloecetes*. She continues: "The *Ricinus* species on the Trochili are typical of the genus apart from the modified mouthparts, and this modification, therefore, must have taken place in the *Ricinus* species of the Trochili after the morphological characters of the genus *Ricinus* had been established; *Trochiloecetes*, closely related to *Ricinus* and restricted to the Trochili, must be a later derivate from a *Ricinus*-like ancestor."

Carriker (1960) revised this group of lice, but created many problems. For example, he established a new family (Trochiliphagidae) for the two genera parasitizing hummingbirds. However, he designated *Trochiloecetes* as genotype. Thus the correct family spelling should be Trochiloecetidae (s. Eichler 1963). Carriker, too, transferred the *Ricinus*-like mallophaga (s. Clay) to a new genus *Trochiliphagus*.

Carriker (1960) believed that *Ricinus* is the progenitor for both, *Trochiloecetes* and *Trochiliphagus*. He ignored that *Ricinus* itself digests blood and not feathers and concluded that both on hummingbirds living genera developed the sucking apparatus because of lack of suitable feathers. Carriker was not aware that the piercing mouth parts of *Trochiloecetes* and *Trochiliphagus* have developed independently. In his mind the change from biting to piercing mouthparts is so essential that it justifies the separation into a new family.

In his monograph Eichler (1963) presents a system for "Mallophaga" within which the "superfamilia" Laemobothrioidea includes two "interfamilias": Laemobothriformia and Riciniformia. Within the latter he defines two families, Ricinidae (with the genus *Ricinus*) and Trochiloecetidae (with the genera: *Trochiloecetes* and *Trochiliphagus*). More recently, Palma (1996) in the Zoological Catalogue of Australia placed all three mentioned genera in the family Ricinidae, as did Price et al. (1993) in the last World Checklist. I will follow this decision here.

Members of *Ricinus* have biting mouthparts and feed on blood of species of Passeriformes s. lat., whereas those of *Trochiloecetes* and *Trochiliphagus* have sucking mouthparts and feed on blood of hummingbirds (Trochilidae).

An earlier paper (Rheinwald 1968) contained a revision of the Old-world species of *Ricinus* and established four species-groups. Nelson (1972) revised the New-world species and established eight species-groups, of which three are identical with the old-world groupings. Therefore six species-groups are recognized with altogether 54 species.

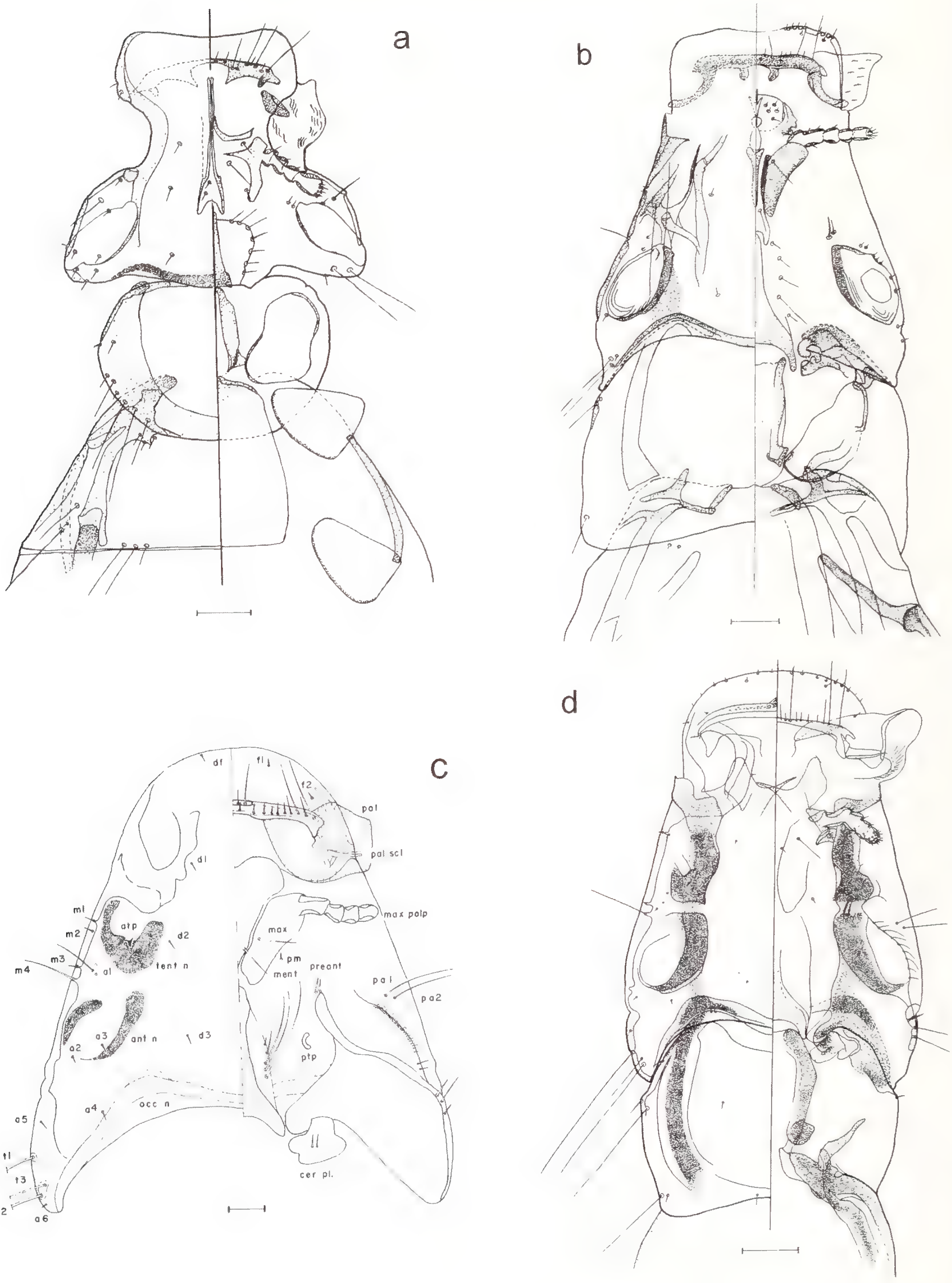
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Fig. 1. Head and prothorax of females a: *Trochiloecetes ochoterenai*?, b: "*Trochiliphagus*", c: *Ricinus brevicapitatis* (from Nelson 1972, plate 2), d: *R. dolichocephalus* (from Rheinwald 1968, Fig. 13). Left from dorsal, right from ventral. Scale bar 0.1 mm.

Carriker (1960) identified at least ten species of *Trochiliphagus* based on minimal size differences and minute changes in shape of the clypeus and prothorax, these differences are often an artefact due to preparation. Generally he says (1960: 331): "There is a generic conformity in the general shape of the head and in the absence of darker markings, following the type of *Ricinus microcephalus*[1] Kellogg, except that the head is longer and usually narrower in the temples."

Nearly all specimens of *Trochiliphagus* which are deposited in US collections were collected by M. A. Carriker. Most of these specimens from a large number of hosts were loaned and studied by Dr. J. Willis-Oniki (Rio Claro, Brasilia) and me in Bonn. Here I noticed the enormous similarity between *Trochiliphagus* and *Ricinus*.

It is the aim of this paper to clarify the position of *Trochiliphagus* within the Ricinidae as far as this is possible with conventional methods.

2. MATERIALS AND METHODS

Drawings were made and measurements taken from the specimens listed in the Appendix. Usually lice are killed and conserved in 70 % ethanol. For mounting on slides they first are hydrated, then treated with weak KOH to resolve the non-chitinized parts of the inside and then embedded in resin. The resolution of the inner parts is necessary; otherwise details of the chitinized skeleton will not be visible. But that means that all characters we know are features of the chitinized skeleton, upon which all species descriptions are based exclusively. For a detailed study of the mouthparts of *Trochiloecetes* and *Ricinus* we possibly also need histological sections.

In my revision of *Ricinus* I figured head and prothorax of every species as well as the terminal segments of the female in dorsal and ventral views. Additionally mandibles, labium and cardo-stipes, gular sclerite and the sternites of pro- and metathorax as well as the male genitalia were presented. Nelson (1972) also followed this format. Therefore I will present here for comparison just these parts in the same view. Additionally claws and limbs of the third leg of a female are measured and drawn.

3. RESULTS

3.1. Head and prothorax

In Figure 1 the head and prothorax of *Trochiloecetes ochoterenai*?, "*Trochiliphagus*", *Ricinus brevicapitatis* Carriker (from Nelson 1972, Table 2) and *R. dolichocephalus* (Scopoli) are presented in the same arrangement. *Ricinus brevicapitatis* is the typical species parasitizing Cotingidae – a bird family close to the base of the Passeriformes. If the classification in Eichler (1963) is accepted, then *Trochiliphagus* and *Trochiloecetes* should be most similar. However, as Figure 1 shows, the highest similarity exists between *R. dolichocephalus* and "*Trochiliphagus*". A special feature of "*Trochiliphagus*" and some species of the *dolichocephalus*-group is that the maxillary palpi exceed far beyond the sides of the head, whereas in all other species the palpi do not reach the border of the head. Additionally, the dorsal lamina of the occiput is well developed.

3.2. Mandibles (Fig. 2)

The only clearly visible feature of the mandible is the articulation. If we follow the sclerites from the articulation further we find in *Trochiloecetes* the structure which Carriker (1960) called the "collar", but it is most likely the remaining portion of the mandible. The mandible of Carriker appears to be part of the basal limb of the palpus. In (b) ("*Trochiliphagus*") homologizing the "mandibles" is highly interpretable. Section series would be necessary to clarify these structures.

3. Gular plate, prosternite and metasternite (Fig. 3)

When we compare again the same forms, *Trochiliphagus* differs significantly from *R. brevicapitatis* and *Trochloecetes* especially in the form of the gular plate and the prosternite. On the other hand, the agreement between "*Trochiliphagus*" and *R. dolichocephalus* is great, even in details in the form of the gular plate and the form of the sclerites in the pro- and metasternite. In Rheinwald (1968), all species of the *dolichocephalus*-group (Figs 13–21, each no. d) generally show the same type as "*Trochiliphagus*", while the species of the *rubeculae*-group (Figs 22–33, each no. d) differ to some degree.

3.4. Labium and cardo-stipes (Fig. 4)

As the figures show, the labium is very uniform in all Ricinidae and therefore contributes little to the systematics of the group. But obviously the cardo-stipes in *Trochiloecetes* and "*Trochiliphagus*" assists considerably the stiletto in its function (see also Fig. 1). The plates behind the labium (cardo-stipes) in *Trochiloecetes* (a) have a rectangular form and in that differ considerably from *Ricinus*. As Figure 1 shows, the ligular sclerite of *Trochiloecetes* is connected directly with the stiletto and

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[1] Which according to my experience (s. Rheinwald 1968) belongs to *R. fringillae*.

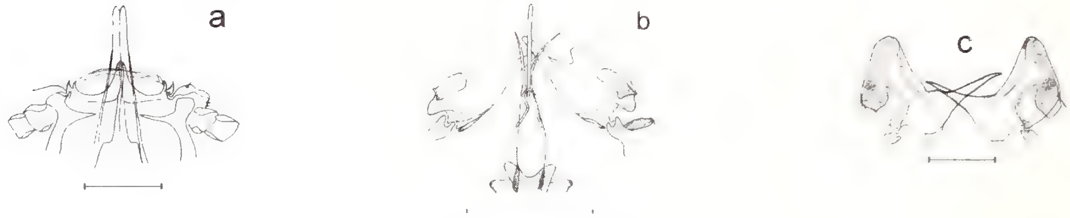

Fig. 2. Mouthparts of a: *Trochiloecetes ochoterenai*?, b: "*Trochiliphagus*", and c: *R. dolichocephalus* (from Rheinwald 1968, Fig. 13). Scale bar 0.1 mm.

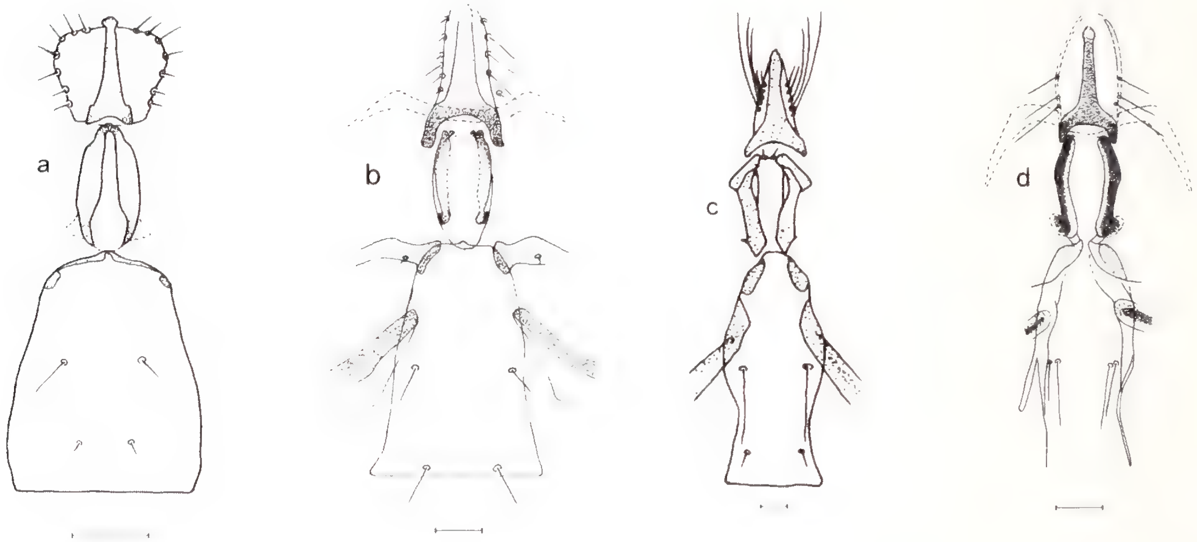

Fig. 3. Gular plate, prosternite and metasternite of a: *Trochiloecetes ochoterenai*?, b: "*Trochiliphagus*", c: *Ricinus brevicapitatis* (after Nelson 1972, combination from plate 2 and 3) and d: *R. dolichocephalus* (from Rheinwald 1968, Fig. 13). Scale bar 0.1 mm.

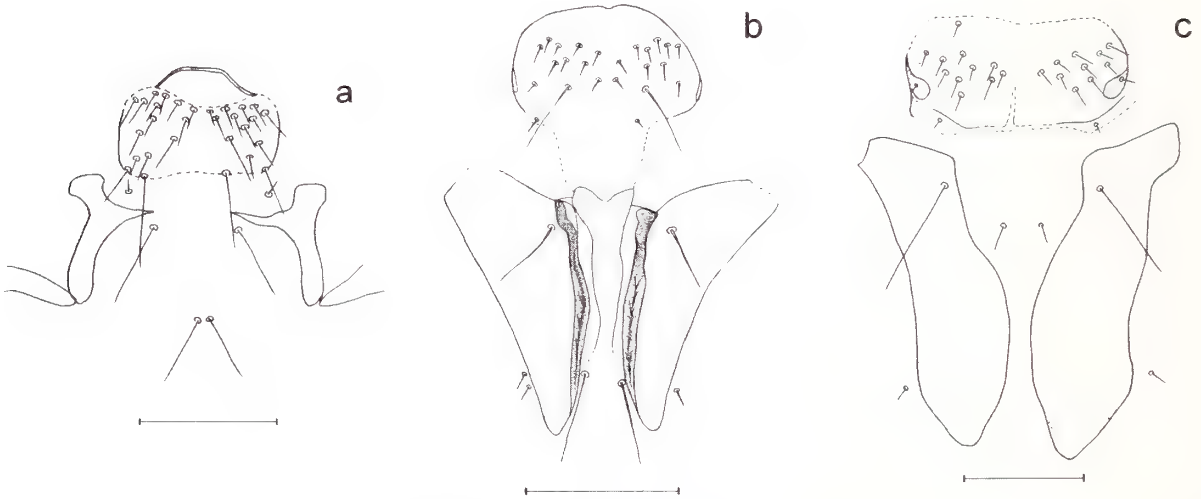

Fig. 4. Labium and cardo-stipes (= maxillar plate according to Nelson 1972) of a: *Trochiloecetes ochoterenai*?, b: "*Trochiliphagus*", and c: *R. dolichocephalus* (from Rheinwald 1968, Fig. 13). In b) an additional intermediate plate. Scale bar 0.1 mm.

at its protruding edges a muscle appears to be attached which stretches well forward (dashed line); obviously the stiletto is bored into the skin by the ligular sclerite. The cardo-stipes is not enlarged, nor sclerotized.

In "*Trochiliphagus*" (b) the ligular sclerite appears not to be connected with the stiletto, but the plate between the cardo-stipes is lengthened into a long, well sclerotized plate. The cardo-stipes in general has the form that is found in all *Ricinus* species (see Nelson 1972; Rheinwald 1968) but it is enlarged and the inner margin is thickened. Obviously the short stiletto of "*Trochiliphagus*" is moved by these plates and bored into the skin of the host. Though it is very difficult to see the single parts of the stiletto in both forms with this preparation method, it seems to be rather clear that the stilettos are moved absolutely differently, which underlines the meaning that the two stilettos have developed convergently.

3.5. Female postabdomen (Fig. 5)

Trochiloecetes differs most; lacking pigmented sternal plates, having well pigmented pleurites to segment VI only and a very small anal tergite (cf. Rheinwald 1968). Arrangement and relative length of setae differs in many respects from that of *Ricinus* species. *Ricinus brevicapitatis* (c) has, like all *Ricinus* species, pigmented sternites, pleurites up to segment VIII and a fringe of small setae at the well-developed anal tergite. "*Trochiliphagus*" and *R. dolichocephalus* are nearly identical, both having the anal tergite surpassing the margin of segment XI and by that the tip of the abdomen, and in the arrangement and the relative length of the tergal and sternal setae.

3.6. Male genitalia (Fig. 6)

In the three species of *Trochiloecetes* the general form is rather simple. The basal plate (cf. Rheinwald 1968, Fig. 1g) is not pointed, the parameres are short and rounded and the genital sclerite is a simple, more or less rectangular structure without significant ornamentation. In *Ricinus arctuatus* (Kellog & Mann) (from Tyrannidae, plate 5 of Nelson 1972) and in other species-groups of *Ricinus* we find many peculiarities in the form of the mesosomal plate, the length of the parameres, the form and ornamentation of the genital sclerite. We find high agreement between "*Trochiliphagus*" and *R. dolichocephalus*. This is especially true in the form of the mesosomal plate and the length of the parameres; in all species of the *dolichocephalus*-group and in "*Trochiliphagus*" the preputial-sac is ornamented with fine structures which are missing in other species-groups.

3.7. Tarsus (Fig. 7)

In my revision of the genus *Ricinus* (Rheinwald 1968) I did not investigate the tarsus. When studying more carefully members of the genus *Trochiloecetes* I noticed that they have huge claws on the last tarsal limb. Thereupon I compared the tarsi of *Trochiloecetes*, "*Trochiliphagus*" and several species-groups of *Ricinus*.

Some general remarks can be made: Obviously within a species the tarsi are morphologically identical, which means that besides individual differences which derive from mounting (as position, angle of the limbs to one another, wrinkles, shrinkages) and bad recognition deriving from the smallness of the object, a series of elements are species-specific. That is especially true for the form of the claws, the form of the outer sclerite at the second tarsal limb, position and size of the two "stonelets"(the homology of which is not clear to me). The form of the inner (second) tarsal limb is species-specific too, even when it is in most cases hard to see and by the position of the outer limb (the angle between outer limb and tibia) as a consequence of mounting is often heavily deformed.

As far as I have material, the species within a species-group of *Ricinus* (*fringillae*- and *rubeculae*-group) appear to correspond in the proportions of the tarsal limbs, the proportions of the claw, the form of the outer sclerite at the tarsal limbs and the tibia as well as in the length of the four large setae at the tip of the inner tibia. That means that members of *Ricinus* and *Trochiloecetes* are well distinguishable by their tarsi. But within the genus *Ricinus* there are also group-specific differences. On the one hand these are the lengths of the claw and the second tarsal limb relative to the total length. On the other hand the form of the outer sclerites of the second tarsal limb and the tibia and the position of the "stonelets" are group-specific.

In connection with the questions in this paper it is of main interest whether *"Trochiliphagus"* shows similarities to *Trochiloecetes* or to *Ricinus*. Table 1 shows that *Trochiloecetes* is separated from all other forms as well by the relative length of the claw as by the relative length of the tarsus. The form of the lateral sclerites of the second tarsal limb and tibia are also clearly different. The tarsus of *Ricinus rubeculae* (Schrank) appears also autapomorphic. It has the relatively smallest claw, the shortest tarsus, and the form of the lateral sclerite differs distinctly.

In opposite to *Ricinus rubeculae*, "*Trochiliphagus*" shows much conformity in the form of the sclerites with *R. fringillae* and *R. dolichocephalus*. While the relative length of the claw agrees well with *R. fringillae* and *R. dolichocephalus*, the relative length of the tarsus differs and appears to be mid-way between *Trochloecetes* and

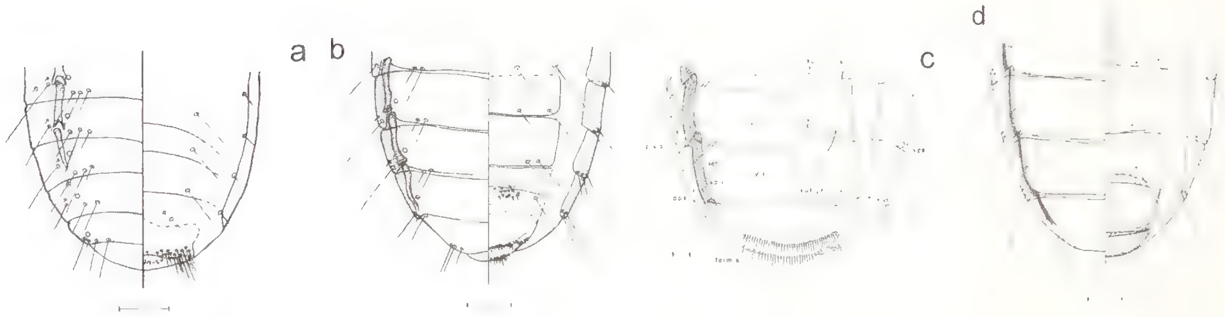

Fig. 5. Abdominal segments and the terminal plates of a: *Trochiloecetes ochoterenai*?, b: "*Trochiliphagus*", c: *Ricinus brevicapitatis* (after NELSON 1972, plate 3) and d: *R. dolichocephalus* (from RHEINWALD 1968, Fig. 13). Left from dorsal, right from ventral. Scale bar 0.1 mm.

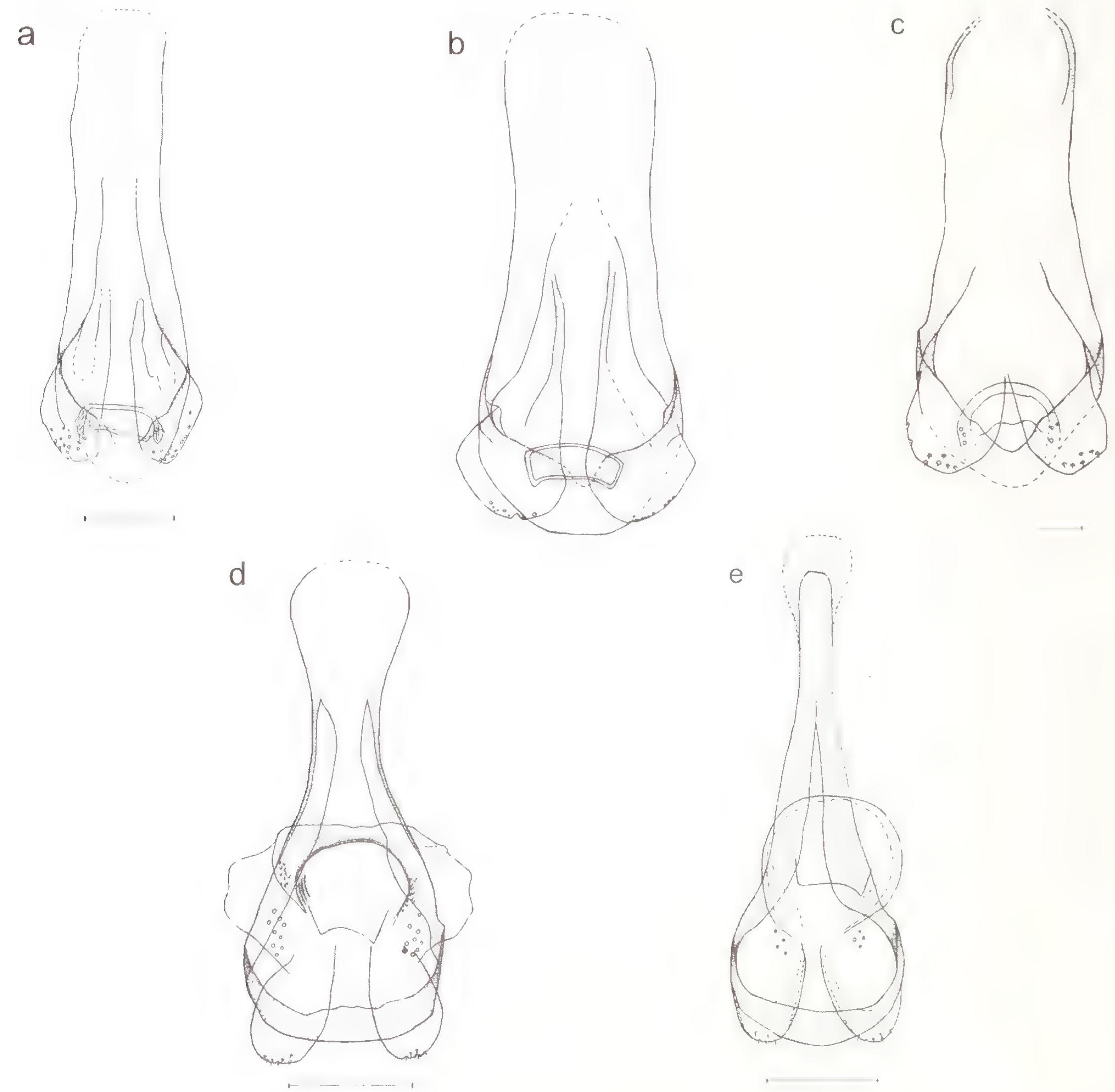

Fig. 6. Male genitalia a: *Trochiloecetes rumpununi*, b: *T. insularis*, c: *T. ochoterenai*, d: "*Trochiliphagus*", e: *Ricinus dolichocephalus* (from RHEINWALD 1968, Fig. 13). Scale bar 0.1 mm.

Table 1. Length of the second tarsal limb and claw, and its relative length in relation to the total length of the two members of Ricinidae living on hummingbirds and of some *Ricinus* species.

	Trochiloecetes	"*Trochiliphagus*"	*R. rubeculae*	*R. fringillae*	*R. dolichocephalus*
total length [mm]	2.18	3.35	3.32	3.02	4.70
length of tarsus [mm]	0.338	0.322	0.178	0.203	0.305
length of the claw [mm]	0.159	0.076	0.038	0.063	0.079
relative length of tarsus	0.155	0.096	0.056	0.067	0.065
relative length of claw	0.073	0.023	0.011	0.021	0.016

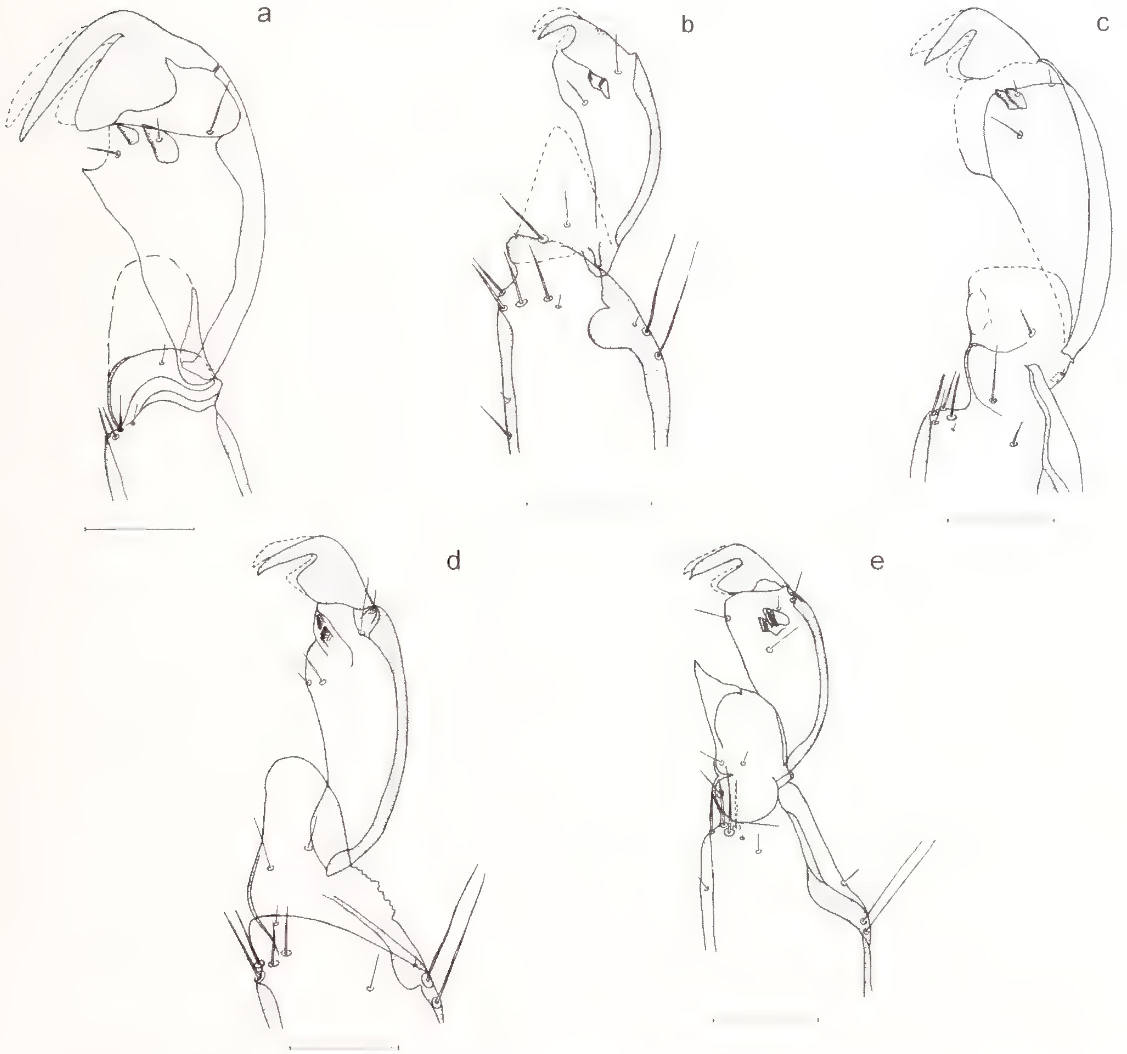

Fig. 7. Claws, two tarsal limbs and tip of tibia of a: *Trochiloecetes ochoterenai*?, b: *Ricinus rubeculus*, c: "*Trochiliphagus*", d: *R. dolichocephalus*, and e: *R. fringillae*. Scale bar 0.1 mm.

Ricinus. One may well suppose that similar to the mouthparts, the tarsi have adapted to the same host-group – the hummingbirds – possibly convergently.

4. DISCUSSION

4.1. Position of "*Trochiliphagus*" within the Ricinidae

For an outgroup comparison members of the family Laemobothriidae seem to be optimal since together with Ricinidae it forms the subclass/superfamily Laemobothriformia. *Laemiobothrion maximum* (Scopoli) recently was investigated by PEREZ et al. (1995) with SEM. But comparable studies in *Trochiloecetes* and *Ricinus* do not exist. SYMMONS (1952) studied the Mallophagan head and also presented figures and descriptions of *Laemobothrion* and description of *Ricinus*. But polarities can not be derived from this. Larger series of *Laemobothrion maximum* were examined, but I was unable to homologize the different parts of the head to derive evolutionary trends. Therefore the question of the polarity between *Trochiloecetes* and *Ricinus* and within *Ricinus* remains unsolved.

Mallophaga as a rule live strictly host-specific, a fact that led to the rule of NITZSCH-KELLOGG. Hummingbirds and songbirds, according to the accepted classifications (e.g., SIBLEY & MONROE 1990) belong to different orders (resp. superorders) that are not closely related. Therefore one should expect that the many species that live on Passeriformes and till now are combined in the genus *Ricinus* should be differentiated significantly in their morphology from those living on Trochiliformes (*Trochiloecetes, Trochiliphagus*). As demonstrated in the figures this is true for *Trochiloecetes*. Not knowing the polarity, these characters can be understood as autapomorphic for *Trochiloecetes*.

In the opposite "*Trochiliphagus*" and *Ricinus* can not be separated from each other. As CLAY (1949) observed, these animals are part of the genus *Ricinus*. The cladistic analysis of MARSHALL (2003), based on 147 morphological characters, supports this idea. Within *Ricinus* all specimens of "*Trochiliphagus*" are best placed within the *dolichocephalus* species-group. If somebody wants to split up the genus *Ricinus* then these separations have to occur along the species-groups that were described by NELSON (1972) and RHEINWALD (1968) earlier. The differentiations of these species-groups relative to the *dolichocephalus*-group are so essential, that the small deviations that accompanied the development of the stiletto and the reduction of the mandibles in "*Trochiliphagus*" appear rather insignificant.

Herewith I place the genus *Trochliphagus* Carriker, 1960 as a junior synonym of *Ricinus* De Geer, 1778. As much as I have seen in the different collections from a variety of hosts there are no consistent morphological differences between these populations. All appear to belong to one morpho-species.

This species should be named *Ricinus jimenezi* Carriker, 1903, though CARRIKER (1960) made *T. lazulus* Carriker 1960 the type-species of *Trochiliphagus*. There exists an older name: *Physostomum lineatum* Osborn, 1896 from *Trochilus colubris* (= *Archilochus colubris*). According to CARRIKER (1960) the three specimens on which the description was based no longer exist. The description makes clear that this is not a *Trochiloecetes*. If the host is correct this should be a "*Trochiliphagus*", though the piercing mouthparts are not mentioned. Under these circumstances the name "*lineatus*" in the family Ricinidae should be suppressed. An application was directed to the International Commission for Nomenclature.

4.2. Primary or secondary?

According to MARSHALL (2003) Laemobotriidae are not close relatives to Ricinidae and therefore not their ancestors. The whole amblycerean louse-family Ricinidae is restricted to Trochilidae and Passeriformes. The differences between *Trochiloecetes* and *Ricinus* fit well in the usual ideas of the relations between Trochilidae as part of the Apodiformes and the Passeriformes. Since the possession of mandibles is symplesiomorphic within the Amblycera, the piercing mouth parts of *Trochiloecetes* is an autapomorphy. If this relation is correct, then *Ricinus jimenezi* must have colonized the Trochilidae secondarily.

4.3. Origin of the secondary colonization

The host-shift onto Trochilidae must have been from a songbird of the families Oriolidae, Meliphagidae, Nectariniidae, Rhipidurinae, Muscicapidae which are the host-families of the *dolichocephalus* species-group. But these bird families all occur exclusively in Africa or Asia. How could it happen that a *Ricinus* from the African-Asian realm colonized a hummingbird in South America? Colonization from an American family of Passerines would be much more likely. But then *Ricinus jimenezi* must show relations to species-groups of *Ricinus* established by NELSON (1972). I could not detect any agreement there.

4.4 Are the Trochilidae a monophyletic taxon?

I do not believe that this is a relevant question, though theoretically it might be that some hummingbirds (the hosts of *Trochiloecetes*) are swift-relatives while others (the hosts of *Ricinus jimenezi*) are songbirds. But CARRIKER (1960) said that he had collected both forms from the same host.

4.5. The development of piercing mouthparts

Hummingbirds have an extremely thick skin. Since the size of the parasites relative to the size of the host is limited, blood-feeding Ricinidae could not grow bigger as they are today. On the smaller hummingbirds these parasites are accordingly smaller. CARRIKER (1960) noted for *Trochiloecetes* a maximal body length of 2.54 mm (see Table 1), while according to his information females of "*Trochiliphagus*" reach 2.57 to 3.8 mm. With this body size the length of the mandibles is not sufficient to open the skin. If therefore a member of Ricinidae were to survive on hummingbirds it had to develop piercing mouthparts. This should be a plausible explanation for the convergent occurrence of two members of Ricinidae with piercing mouthparts on hummingbirds.

For *Trochloecetes* this explanation may be evident. Because these are the original parasites, they should have evolved on hummingbirds since their separation from swifts and could gradually evolve a stiletto in addition to the mandibles; as soon as this stiletto was completely functional the mandibles could be reduced.

For the secondary settler, *Ricinus jimenezi,* great obstacles must have arisen. When it moved from songbirds to hummingbirds it had mandibles and certainly no stiletto because it did not need it for living on songbirds. But with its mandibles it could not pierce the skin of a hummingbird. Therefore it should have starved and a secondary infestation would not have happened. If it would have found thinner parts of skin where it may have survived some time why should it then evolve a stiletto?

Even when the membership of "*Trochiliphagus*" to *Ricinus* and here to the *dolichocephalus* species-group seems to be evident, it is absolutely unclear how we can imagine the procedure of this secondary colonisation. The question of the offspring of *Ricinus jimenezi* and therefore its relations to *Ricinus* and perhaps the reconstruction of the history of its development might be a fascinating case for the application of modern enzymatic or DNA-techniques. The biggest problem here may be the procurement of relevant Mallophaga which in no case are abundant and in many cases are known to science just by one specimen. Normally the eggs of *Ricinus* at the bases of the feathers of neck and anterior breast are so conspicuous that with some experience it is easy to detect those birds where it is worth while searching for adults.

4.6. Plasticity of the mouthparts

The occurrence of biting and piercing mouthparts within the genus *Ricinus* throws new light on the question what value mouthparts have as characters for phylogenetic discussions. It is meanwhile common sense that Ischnocera and Anoplura are sister-groups (BARKER et al. 2003; HOPKINS 1949; WEBB 1946). In the Anoplura sucking mouthparts developed for the first time in the Phthiraptera. In the other large group of the Phthiraptera, the Amblycera, a stiletto evolved twice, both within the Ricinidae. On the one hand in *Trochiloecetes*, which obviously is the characteristic Ricinidae of the Trochilidae, and on the other hand within *Ricinus* when one of its members secondarily colonised Trochilidae. That means that piercing mouthparts evolved at least three times within Phthiraptera.

But if such fundamental alterations are in principle possible, what general value has mouthparts as a phylogenetic feature? We have examples from other animal classes, such as birds, in which alterations in the mouthparts within small taxonomic units are of similar dimensions. As a consequence in future we should leave out features of the mouthparts in our data sets for the analysis of phylogeny.

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APPENDIX

Investigated material

The Natural History Museum, London

Trochiliphagus hirsutus Carriker ♂ Paratype	*Glaucis hirsuta*, Aripo Valley, Trinidad, 14.IV.1960, TRVL. 4505, Brit. Mus. 1963–351
Trochiliphagus hirsutus Carriker ♀	*Glaucis hirsuta*, Aripo Valley, Trinidad, Aitken coll. Brit. Mus. 1963–351
Trochiloecetes rupununi Carriker ♀	*Phaethornis superciliosus* (AMH 36), Belize, Aguacate, 4.V.1979, C. Lyal and A. Hutson
Trochiloecetes rupununi Carriker ♀, ♂	*Phaethornis superciliosus*, 42984, Mosqueiro Ferry, Benevides, Brazil, 25.X.1968, T. Aitken, ML.17, Brit. Mus. 1970–726
Trochiloecetes insularis Carriker ♂ Paratype	*Glaucis hirsuta*, Aripo Valley, Trinidad, 5.VII. 1960, TRVL. 4622, Brit. Mus. 1963–351
Trochiloecetes insularis Carriker 3 larvae	*Glaucis hirsuta*, Aripo Valley, Trinidad, 5.VII. 1960, TRVL. 4622, Brit. Mus. 1963–351
Trochiloecetes insularis Carriker ♀, 1 larva	*Glaucis hirsuta*, Aripo Valley, Trinidad, 17.III. 1961, T. Clay, No. 194, Brit. Mus. 1963–351
Ricinus dolichocephalus (Scopoli) 3 ♀ Neoparatype	*Oriolus. o. oriolus*, N.E. Poland, VIII 1935, 4190, Brit. Mus. 1951–171

Personal material

Trochiloecetes ochroterenai? 1 ♀, 1 ♂	*Selasphorus rufus*, Nationalpark Desierto de los Leones, 30 km w. von Mexico City, VIII 1971, leg. Poley
Trochiloecetes spec. 1 ♀	*Eugenes fulgens*, Nationalpark Desierto de los Leones, 30 km w. von Mexico City, VIII 1971, leg. Poley
Ricinus rubeculae (Schrank) 1 ♂, 3 ♀	*Luscinia svecica cyanecula*, Modracek, Pakvice, CSR, 4.IV.1955, leg. F. Balat
Ricinus fringillae De Geer 1 ♀	*Fringilla coelebs*, Obergurgl, Ötztal, Österreich, 1.IX.1968, leg. A. Aichhorn

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The Freshwater Mite *Porolohmannella violacea* (Kramer, 1879) (Acari: Halacaridae), Description of Juveniles and Females and Notes on Development and Distribution

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Abstract. The description of female *Porolohmannella violacea* (Kramer, 1879) is supplemented and the development of external characters from larva to adult described. Beside an increase in size and number of setae from instar to instar, similar to that in other halacarid species, there is a marked difference in the growth in length of the palp and leg segments. Larva and protonymphs have epimeral pores. Data on geographical distribution are summarized. According to present records, *P. violacea* is restricted to the northern hemisphere, nonetheless, it is expected to be found in the south, too.

Keywords. Freshwater halacarid, *Porolohmannella*, development, distribution.

1. INTRODUCTION

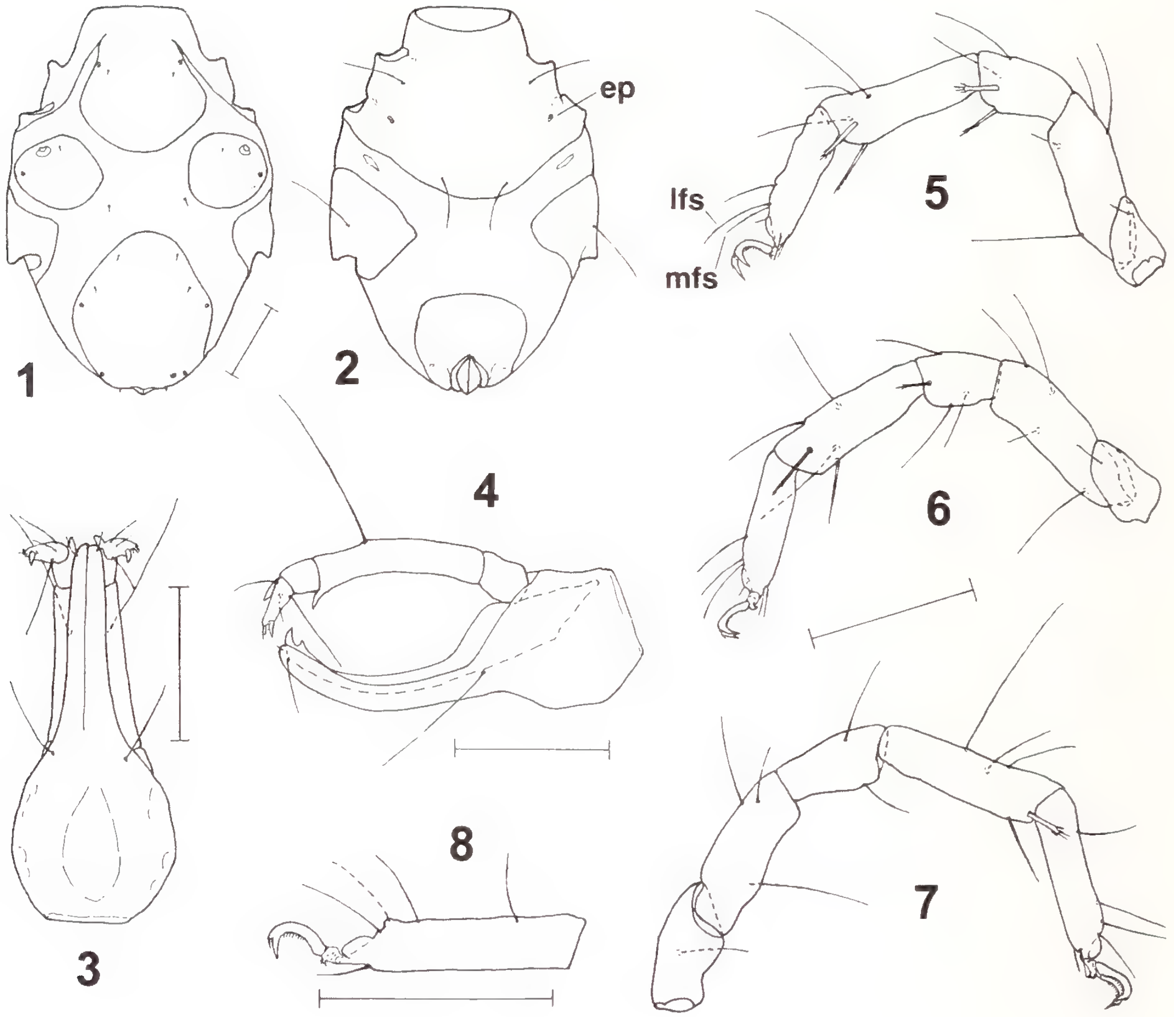
Halacarid mites are primarily marine but a few species live almost exclusively in continental freshwater. KRAMER (1879) was the first to describe a halacarid from freshwater, *Leptognathus violacea*, a rather large species characterized by a long, slightly curved rostrum and palps, in all strikingly similar to the marine genus *Leptognathus* Hodge, 1863, and a violet to pink integument, hence the name *violacea* (cf. KRAMER 1879). The species, described from Thuringia, Germany, turned out to be wide-spread in Europe, as documented by the large numbers of citations (cf. K. VIETS 1956; K. O. VIETS 1978, 1987).

The name *Leptognathus* proved to be pre-occupied and LOHMANN (1901) proposed a new name, *Trouessartella* Lohmann, 1901. This was pre-occupied, too, and thereupon TROUESSART (1901) introduced *Lohmannella* Trouessart, 1901.

In the following decades the number of both marine and freshwater halacarid species increased. Karl VIETS (1927, 1933) separated the freshwater species, all with external genital acetabula, from the marine species with internal acetabula, and distinguished between the families Halacaridae Murray, 1877 and Porohalacaridae Viets, 1933, the former including the marine taxa, the latter the freshwater taxa. Accordingly, K. VIETS (1927, 1933) distinguished between a marine genus *Lohmannella*, in the Lohmannellinae Viets, 1927, and a freshwater genus, for which he introduced the name *Porolohmannella* Viets, 1933, with the type species *P. violacea* (Kramer), and the subfamily Porolohmannellinae Viets, 1933.

The division into Halacaridae and Porohalacaridae, solely based on the position of the genital acetabula, external or internal, was abandoned by NEWELL (1947), BARTSCH (1973) and PETROVA (1974, 1981). In several species of the marine genera *Acarothrix* Bartsch, 1990, *Halacarellus* Viets, 1927, *Halacaroides* Bartsch, 1981, *Isobactrus* Newell, 1947, and *Thalassarachna* Packard, 1871 males have external but females internal acetabula (BARTSCH 2004, and in press). External genital acetabula are ion-permeable areas with osmoregulatory function (BARTSCH 1973; ALBERTI 1977, 1979). In marine halacarids one to three pairs of acetabula are present, in freshwater forms often more than three. The genital acetabula may be large, e.g., in the genera *Halacarus* Gosse, 1855 and *Thalassarachna*, or small, as in most species of *Copidognathus* Trouessart, 1888 and *Simognathus* Trouessart, 1889. In a few marine species, unusual enlargement is documented. Many, though not all halacarid mites living in freshwater have external genital acetabula.

Species of freshwater genera differ from marine ones both in the position of the genital acetabula and in their integument. The plates are thin, they show no coarse sculpturing or raised areolae, no rosette pores; they often are rather uniformly ornamented, with a reticulate or foveate pattern, and have tiny evenly spread canaliculi cross the integumental layers. The position of the genital acetabula as well as the structure of the integument and ornamentation of the plates certainly are influenced by physical and chemical environmental features, as in other meiofaunal taxa, e.g., in ostracods (MEISCH 2000).



Figs 1–8. *Porolohmannella violacea*, larva, **1**, idiosoma, dorsal; **2**, idiosoma, ventral; **3**, gnathosoma, ventral; **4**, gnathosoma, lateral; **5**, leg I, medial; **6**, leg II, medial; **7**, leg III, medial; **8**, tarsus III, lateral (medial parambulacral seta and claw omitted, dorsomedial fossary seta in broken line). (ep, epimeral pore; lfs, dorsolateral fossary seta; mfs, dorsomedial fossary seta) Scale = 50 µm.

Independent of the position of the genital acetabula, *Porolohmannella* and *Lohmannella* proved to differ in a number of other characters, in the number of setae on the epimeral plates and genitoanal plate, the number and arrangement of setae on the palps and gnathosoma, the shape of the pharyngeal plate, the position of the solenidion on tarsus II, and absence or presence of a carpite (cf. BARTSCH 1989). The state of these characters is expected to be independent of environmental parameters.

Recently, in a small pond near Hamburg, Germany, numerous females and juveniles of *Porolohmannella violacea* were found. The development of external characters, from instar to instar, has been studied in several marine species (BARTSCH 1998, 2003) but to date in no representative of a freshwater halacarid genus. The larva, nymphs and female of *P. violacea* are now described, the character development outlined and compared with marine halacarids.

2. MATERIAL AND METHODS

The material studied was collected in June, July and August 2006 in northern Germany, north of Hamburg, in a shallow pond adjacent to a helocrene swamp area. The pond is approximately 10x20 m (width x length), on the northern border there are small bushes, mainly willows

(*Salix* sp.), rarely more than 3 m in height, along the southern border most trees have been removed. In the shallow water there is a mass occurrence of the moss *Fontinalis howellii* Renauld & Cardot.

Obvious macrofaunal elements in the pond are the snails *Lymnaea stagnalis* (Linnaeus, 1758) and *Planorbarius corneus* (Linnaeus, 1758). Amongst the meiofauna living between the moss mites were very abundant, viz., the halacarids *Porohalacarus alpinus* Thor, 1910 and *Porolohmannella violacea* and the oribatid mite genus *Hydrozetes* Berlese, 1902; Hydrachnidia and the halacarid mites *Soldanellonyx monardi* Walter, 1919 and *Lobohalacarus weberi* (Viets & Romijn, 1924) were rare. Other meiofaunal taxa were rotatorians, turbellarians, nematodes, oligochaetes, tardigrades, and larvae of insects (ceratopogonids and chironomids); copepods or ostracods were almost lacking.

In January, February and March 2006 the mean monthly temperature was below 1 °C (Deutscher Wetterdienst 2006). June and July 2006 were characterized by high temperature and intense, long-term sunshine. July, with several days beyond 30 °C, had higher temperature and more sunshine than ever registered since regular documentation of meteorological data (which started a century ago). The sunshine period, with up to 16 hours a day, was 50 % beyond long-term mean July values. In both June and July rain was considerably below average. August was extremely wet, with two to four times more rain than usual (Deutscher Wetterdienst 2006).

Porolohmannella violacea was extracted from moss samples. Ten individuals of each instar (larva, protonymph, deutonymph, female) were studied in detail. Abbreviations used in the descriptions are: AD, anterior dorsal plate; AE, anterior epimeral plate; ds-1 to ds-6, first to sixth pair of dorsal setae of idiosoma, numbered from anterior backward; EI to EIV, epimeral plate(s) I to IV; GA, genitoanal plate; GO, genital opening; GP, genital plate; OC, ocular plate(s); P-2 to P-4, second to fourth palpal segment; pas, parambulacral seta(e); PD, posterior dorsal plate; PE, posterior epimeral plate(s); pgs, perigenital setae. The epimeral plates, legs and their segments are numbered I to IV. The leg segments are trochanter, basifemur, telofemur, genu, tibia, and tarsus. The setation formula of the legs presents the number of setae from trochanter to tarsus. The given number of setae of the tarsi includes the solenidion and parambulacral setae. The position of a seta is given in a decimal system with reference to the length of the relevant structure, from its anterior to posterior or proximal to distal end. Voucher specimens of each instar are deposited in the Zoological Museum in Hamburg.

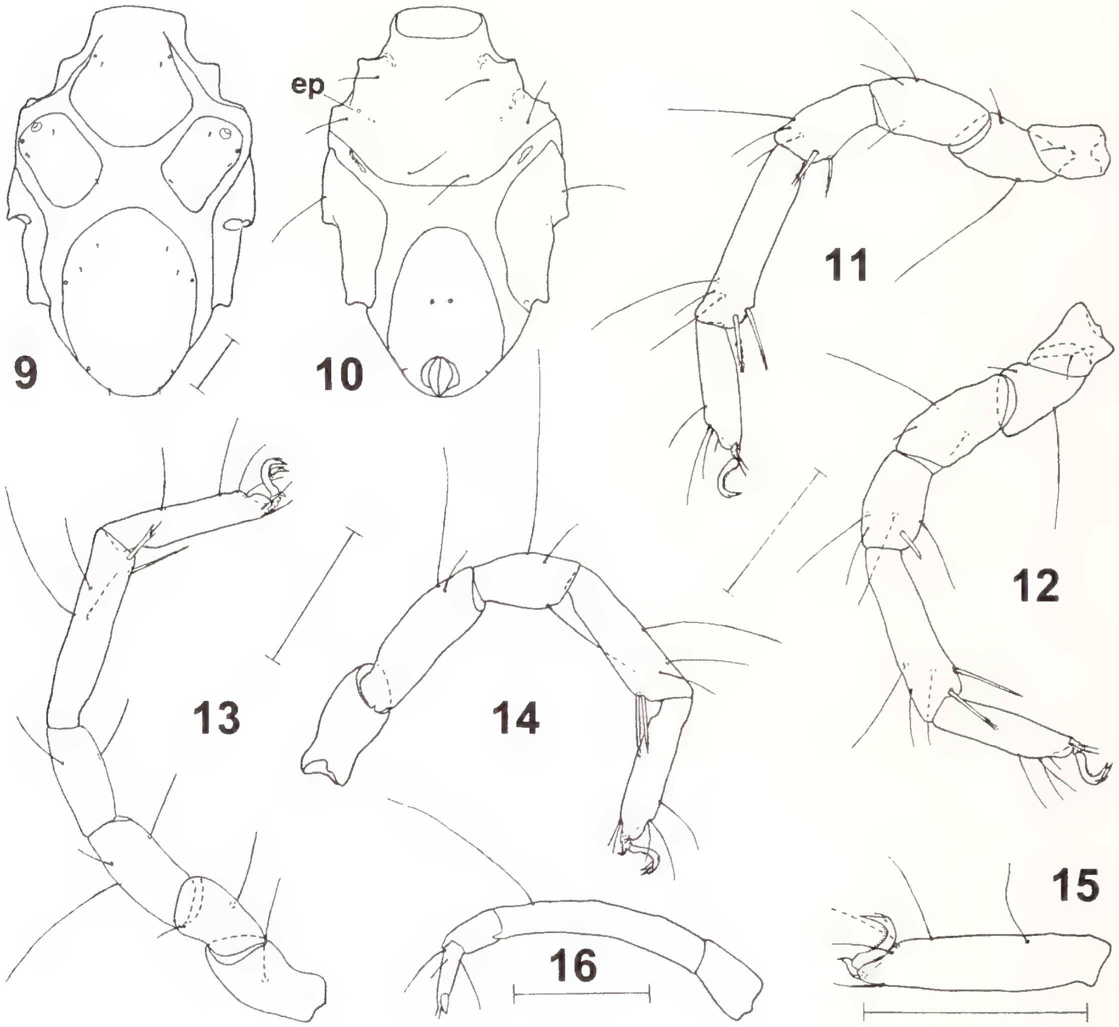
3. DESCRIPTION

3. 1. Larva (Figs 1–8)

Idiosoma. Length 207–277 µm. Idiosoma pale, almost transparent, with pair of small spots of black eye-pigment. Dorsal plates with delicately reticulate ornamentation, each polygon about 5–7 µm in diameter. Anterior margin of AD truncate (Fig. 1). OC rounded, slightly wider than long. PD 1.2 times longer than AD. Idiosoma with four pairs of gland pores, one pair on AD, one on OC, and two pairs on PD. Pore canaliculus immediately posterior to gland pore of OC. Dorsal setae tiny. Pair of ds-1 on AD, ds-2 on OC, ds-3 in striated integument, ds-4 and ds-5 on PD, both anterior to the level of third pair of gland pores, ds-6 in posterior margin of PD. Part of anal sclerites seen in dorsal aspect. AE with pair of epimeral pores (Fig. 2), each slightly ovate and 4–5 µm in diameter, and two pairs of long, slender ventral setae. PE short, epimeral plate IV lacking; PE with single pair of slender setae. Anus in posterior end of idiosoma.

Gnathosoma. Length 117–123 µm, 0.44–0.50 of length of idiosoma. Rostrum slender, about 1.5 times longer than gnathosomal base. Gnathosomal base faintly ornamented. Pharyngeal plate large, extending almost to basal margin (Fig. 3). Tectum slightly concave. Basal pair of maxillary setae long, inserted near base of rostrum, apical pair of maxillary setae near tip of rostrum, adjacent to two pairs of rostral setae. Palps four-segmented. P-2 cylindrical, with conspicuously long seta at 0.68 or about 18 µm proximal to end of segment; apically with a ventromedial lamellar process (Fig. 4). P-3 with dorsomedial lamellar process. P-4 with three slender setae in a basal whorl, a short spine, two stout setae, about 7 µm long, and one setula. Chelicerae elongate; small apical claw dentate.

Legs. With three pairs of five-segmented legs; basi- and telofemora fused. Number of setae per segment: legs I and II, 1, 1+3 (basi- + telofemur), 4, 5, 6; leg III, 1, 1+2, 2, 5, 6. No variation in the 10 larvae studied. Tibiae I to III 1.2, 1.1 and 1.1 times longer than tarsi. Pair of ventral setae on genu and tibia I pectinate (Fig. 5). Genu II with single pectinate seta and tibiae II and III each with pair of ventral setae (Figs 6 and 7). All tarsi with pair of small fossa membranes. Tarsus I with dorsolateral papilla proximal to dorsal fossary seta. Solenidion on tarsus I and II in dorsolateral position immediately adjacent to fossa membrane, about 6 µm long. Dorsolateral fossary seta on tarsus I distinctly longer than dorsomedial seta. On tarsi II and III no such difference in length of fossary setae. On tarsus III interval between basal seta and dorsal fossary seta about 20 µm, distance from basal seta to basis of tarsus somewhat more than height of tarsus; basal seta at 0.27 relative to length tarsus (Fig. 8). All tarsi end with pair of



Figs 9–16. *Porolohmannella violacea*, protonymph, **9**, idiosoma, dorsal; **10**, idiosoma, ventral; **11**, leg I, medial; **12**, leg II, medial; **13**, leg III, medial; **14**, leg IV, medial; **15**, tarsus III, lateral (medial parambulacral seta and claw omitted, dorsomedial fossary seta in broken line); **16**, palp, lateral. (ep, epimeral pore) Scale = 50 µm.

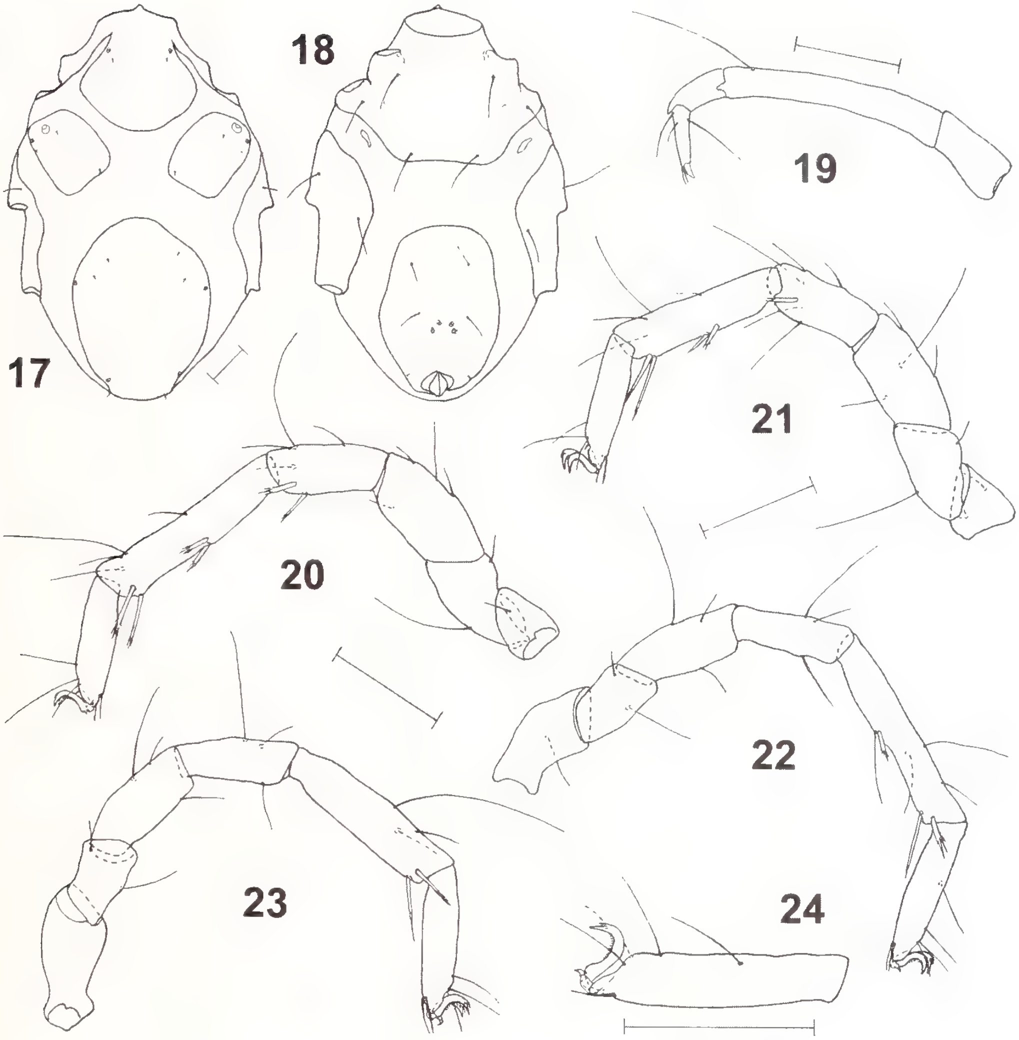
parambulacral setae. Tarsi with paired claws. Claw pecten with short tines. Central sclerite minute, on tarsus III with delicate upper tooth.

3. 2. Protonymph (Figs 9–16)

Idiosoma. Length 301–347 µm. Idiosoma pale, translucent; gut contents with red spots. Idiosoma with two lateral and one median spot of eye pigment. Dorsal plates delicately reticulate. Anterior margin of AD truncate (Fig. 9) or with minute frontal process. OC longer than wide. PD 1.3 times longer than AD. Pair of ds-3 on OC. AE with pair of small epimeral pores (Fig. 10), 3–4 µm in diameter, and three pairs of slender setae. PE including epimeral plates III and IV; a single ventral (marginal) seta present. Genital plate and anal plate fused to GA; this plate with one pair of external genital acetabula which are 4 µm in diameter.

Gnathosoma. Length 145–161 µm, i.e., 0.43–0.49 of length of idiosoma. Seta on P-2 at 0.81 (Fig. 16); distance from seta to end of P-2 15 µm.

Legs. With four pairs of legs, legs I to III six-segmented (Figs 11–13), leg IV five-segmented (Fig. 14). Leg chaetotaxy: legs I and II, 1, 2, 3, 5, 5, 6; leg III, 1, 2, 3, 2, 5, 6;



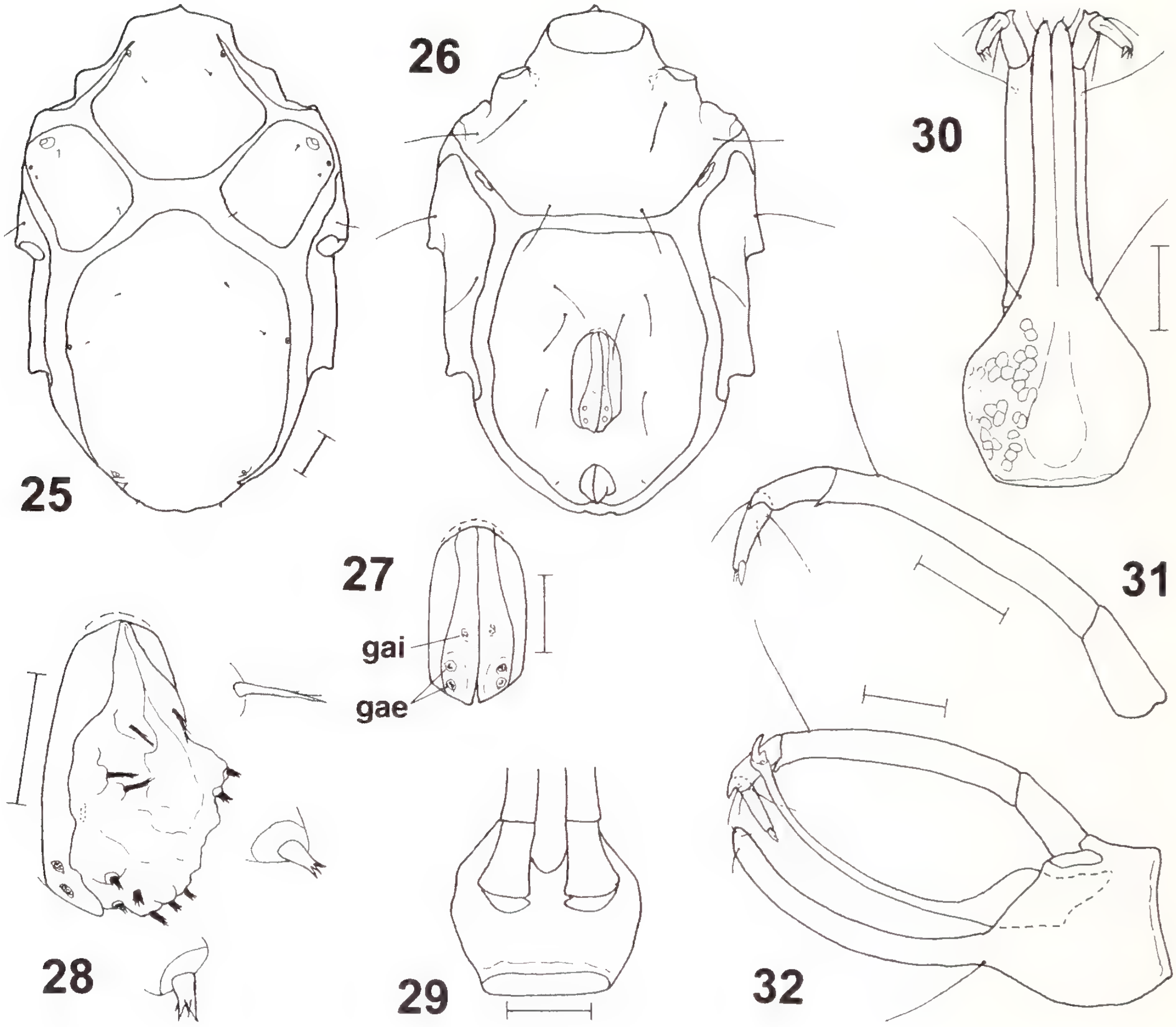
Figs 17–24. *Porolohmannella violacea*, deutonymph, **17**, idiosoma, dorsal; **18**, idiosoma, ventral; **19**, palp, lateral; **20**, leg I, medial; **21**, leg II, medial; **22**, leg III, medial; **23**, leg IV, medial; **24**, tarsus III, lateral (medial parambulacral seta and claw omitted, dorsomedial fossary seta in broken line). Scale = 50 µm.

leg IV, 0, 0+2 (basi- + telofemur), 3, 5, 5. Tibiae I to IV 1.5, 1.3, 1.2 and 1.1 times longer than tarsi; telofemora I to III 1.1–1.2 times longer than genua. Genu and tibia I each with pair of bipectinate setae (Fig. 11). Genu II with single pectinate seta. Tibiae II to IV each with pair of ventral setae; on tibia III ventromedial seta coarsely pectinate and somewhat shorter than ventrolateral seta; on tibia IV both setae similar in size and not markedly pectinate. Paired fossary setae on tarsus I dissimilar in length, on tarsi II to IV almost equal in length. Basal seta on tarsus III at 0.38 relative to length of tarsus (Fig. 15), or 1.5 times height of tarsus; interval between basal seta and dorsal fossary seta 20 µm.

3. 3. Deutonymph (Figs 17–24)

Idiosoma. Length 440–487 µm. Idiosoma with three spots of eye pigment. Dorsal and ventral plates reticulate. AD with small frontal spine (Fig. 17); AD about as long as wide. OC with cornea, two pairs of minute setae, gland pore and pore canaliculus. Length of PD about 1.4 times that of AD. AE with three pairs of ventral setae; epimeral pores lacking. PE with short dorsal seta and two long ventral setae. GA with two pairs of setae, situated anterior to two pairs of genital acetabula (Fig. 18). Acetabula 3–4 µm in diameter.

Gnathosoma. Length 195–204 µm, i.e., 0.41–0.45 of length of idiosoma. Seta on P-2 at 0.85 (Fig. 19), or 15 µm removed from apical end.

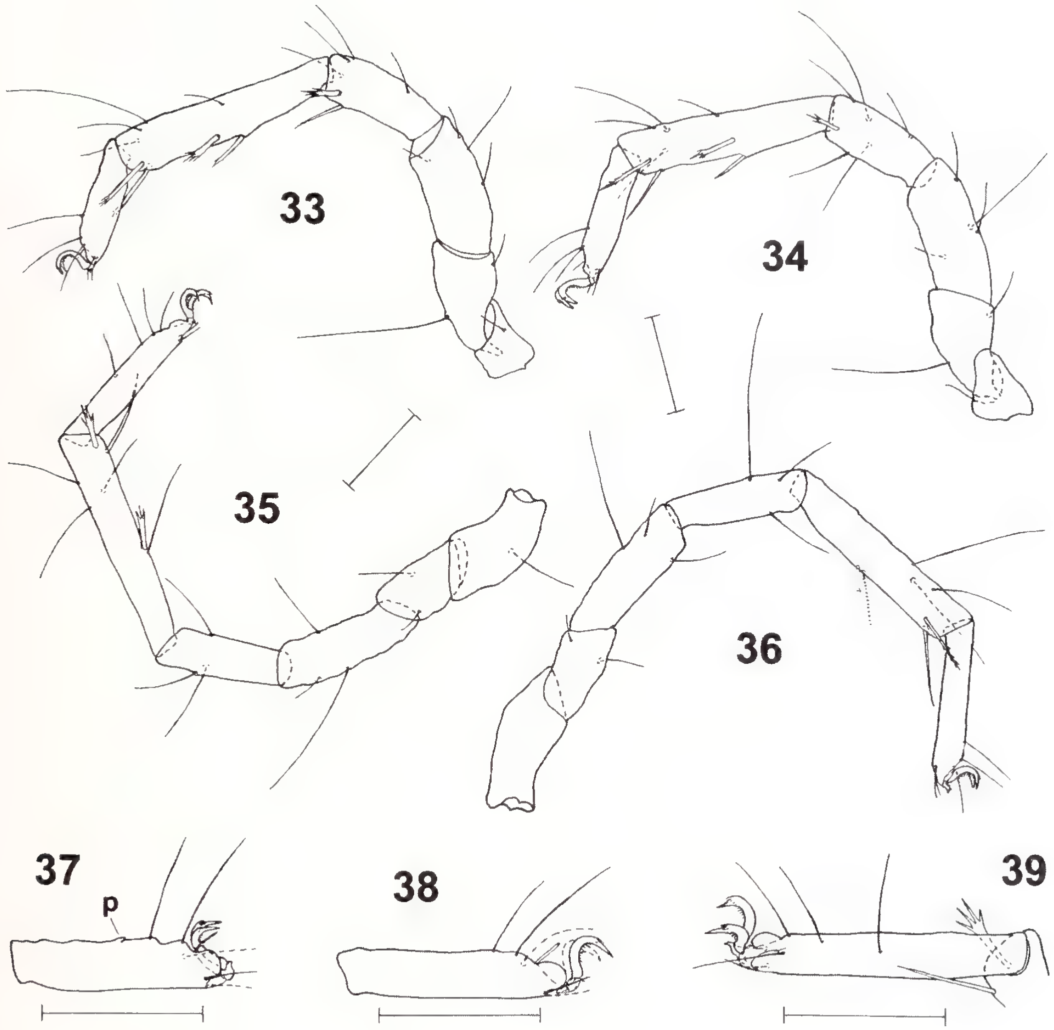


Figs 25–32. *Porolohmannella violacea*, female, **25**, idiosoma, dorsal; **26**, idiosoma, ventral; **27**, genital sclerites; **28**, ovipositor with genital spines; **29**, gnathosomal base, dorsal; **30**, gnathosoma, ventral; **31**, palp, lateral; **32**, gnathosoma, lateral. (gae, external genital acetabula; gai, internal genital acetabulum) Scale = 50 µm.

Legs. All four pairs of legs six-segmented. Tibiae of legs I to IV 1.7, 1.5, 1.4 and 1.3 times longer than corresponding tarsi. Telofemora of all legs about 1.1 times length of genua. Leg chaetotaxy as summarized in Table 1. Genua I and II with two and one pectinate setae, respectively. Tibia I in general with four ventral pectinate setae (Fig. 20), rarely with three such setae and one of mid-segmental setae being absent. Tibia II mostly with three, rarely with four ventral setae (Fig. 21). Tibia III with four ventral setae, two of them short and pectinate, one seta slender and smooth and one rather stout but without distinct pectination (Fig. 22). Tibia IV with single pair of generally long ventral setae (Fig. 23). On tarsi I and II dorsolateral fossary seta longer than dorsomedial one, on following tarsi these fossary setae similar in size. On tarsus III distance between basal seta and dorsal fossary seta 20 µm; this basal seta at 0.46 relative to length of tarsus (Fig. 24); distance between basal seta and basal edge of tarsus slightly more than height of tarsus.

3. 4. Female (Figs 25–39)

Idiosoma. Length 525–590 µm. Integument of idiosoma, gnathosoma and legs pink to violet, gut contents red-brown. With three spots of eye pigment, a pair on OC and a single one on AD. Dorsal and ventral plates distinctly reticulate, mesh size 5–8 µm. AD slightly wider than long (Fig. 25). OC longer than wide. Length of PD about 1.7 times that of AD. AE wider than long, with three pairs of ventral setae. PE with short dorsal seta and two long ven-



Figs 33–39. *Porolohmannella violacea*, female, **33,** leg I, medial; **34**, leg II, medial; **35**, leg III, medial; **36**, leg IV, medial; **37**, tarsus I, lateral (medial parambulacral seta and dorsomedial fossary seta in broken line); **38**, tarsus II, lateral (medial parambulacral seta, claw and dorsomedial fossary seta in broken line); **39**, end of tibia and tarsus III, dorsolateral. (p, papilla) Scale = 50 µm.

tral setae (Figs. 25 and 26). GA large, dominating ventral aspect; plate with three pairs of slender perigenital setae, two pairs anterior to GO, one pair lateral to GO. GO almost in middle of GA. Genital sclerites with two pairs of external genital acetabula, each acetabulum about 5 µm in diameter. A third pair of similar-sized genital acetabula in internal position, on inner flank of genital sclerites (Fig. 27). Ovipositor short, with basal pair of bristle-like setae and five pairs of short apical spines (Fig. 28). Basal pair 15 µm long and delicately pennate. Apical pairs of genital spines 7–9 µm long and tri- or quadrifid; two anterior pairs somewhat longer (9 µm) than three posterior pairs of apical genital spines. Anus in ventral position. Females with zero to three eggs.

Gnathosoma. Length 252–275 µm, 0.45–0.48 of length of idiosoma. Gnathosomal base coarsely foveate (Fig. 30). Arrangement of maxillary setae as in larva (Fig. 30). Tectum concave (Fig. 29). P-2 and P-3 with ventromedial and dorsomedial spiniform process, respectively (Fig. 32). Seta on P-2 at 0.86 (Figs 31 and 32), 20 µm proximal to end of that segment.

Legs. Tibiae of legs I to IV 1.9, 1.6, 1.5 and 1.3 times longer than their tarsi; telofemora 1.1–1.2 times longer than genua. Chaetotaxy as summarized in Table 2. Genu and tibia I with one and two pairs of ventral setae, respectively, ventromedial setae distinctly pectinate (Fig. 33), ventrolateral setae weakly pectinate. Genu and tibia II with one and three to four pectinate setae, respectively (Fig. 34).

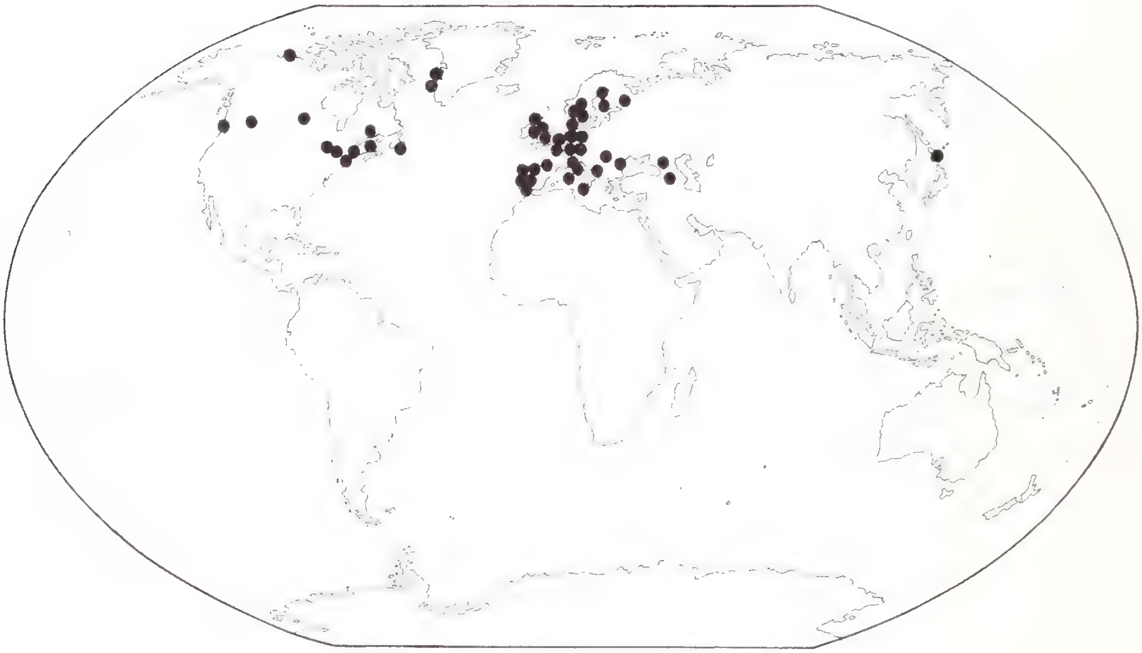


Fig. 40. Geographical distribution of *Porolohmannella violacea.*

Table 1. *Porolohmannella violacea*, deutonymph. Leg segments and their number of setae (number of cases of a given variant in brackets).

segment	1	2	3	4	5	6
leg I	1(20)	2(20)	3(2),4(17),5(1)	6(20)	7(7),8(13)	6(20)
leg II	1(20)	2(20)	3(1),4(19)	6(20)	7(18),8(2)	6(20)
leg III	1(20)	2(20)	3(20)	3(20)	7(20)	6(20)
leg IV	0(20)	2(20)	3(20)	3(20)	5(20)	5(20)

Table 2. *Porolohmannella violacea*, female. Leg segments and their number of setae (number of cases of a given variant in brackets).

segment	1	2	3	4	5	6
leg I	1(20)	2(20)	4(20)	6(20)	7(1),8(19)	6(20)
leg II	1(20)	2(20)	4(20)	6(20)	7(3),8(17)	6(20)
leg III	1(20)	1(1),2(17),3(2)	3(20)	3(20)	7(20)	6(20)
leg IV	0(19),1(1)	2(20)	2(1),3(19)	3(20)	5(3),6(12),7(5)	5(20)

Table 3. *Porolohmannella violacea.* Number of idiosomal setae, epimeral pores, epimeral plates, and genital acetabula (internal and external) in each instar. (–, GP absent in larva. Changes from one instar to the other underlined and in bold).

	L	PN	DN	Ad
AE, pairs of setae	2	**3**	3	3
AE, pairs of epimeral pores	1	1	**0**	0
PE including epimeral plates	EIII	EIII,**EIV**	EIII,EIV	EIII,EIV
PE, number of setae	1	1	**3**	3
GP, pairs of setae	–	0	**2**	**3**
GP, pairs of acetabula	–	1	**2**	**3**

Table 4. *Porolohmannella violacea.* Leg chaetotaxy of larva\protonyph\deutonymph\female. (-, leg IV absent in larva. Single cases omitted, rare variants in parentheses. Changes from one instar to the other underlined and in bold).

	leg I	leg II	leg III	leg IV
	L\PN\DN\Ad	L\PN\DN\Ad	L\PN\DN\Ad	L\PN\DN\Ad
trochanter	1\1\1\1	1\1\1\1	1\1\1\1	-\0\0\0
basifemur	1**2**\2\2	1**2**\2\2	1**2**\2\2(-3)	-\0\2\2
telofemur	3\3\(3-)**4**\4	3\3\4\4	2**3**\3\3	-\2\3\3
genu	4**5**\6\6	4**5\6**\6	2\2\3\3	-\3\3\3
tibia	5\5\7-8\8	5\5\7(-8)\(7-)**8**	5\5\7\7	-\5\5\(5-)**6**(**-7**)
tarsus	6\6\6\6	6\6\6\6	6\6\6\6	-\5\5\5

Tibia III with four ventral setae, ventromedial setae short and pectinate (Fig. 35). Tibia IV with three dorsal and two to four ventral setae (Fig. 36); pair of apical ventral setae always present; number of mid-segmental setae, one pectinate, one slender, variable, often different on right and left leg. Solenidia on tarsi I and II (Figs 37 and 38) in dorsolateral position, adjacent to fossa membrane, 10 and 9 µm in length, respectively. On these tarsi dorsomedial fossary seta distinctly shorter than dorsolateral seta. Tarsus I with papilliform process proximal to dorsal fossary seta (Fig. 37). Basal seta of tarsus III almost in middle of segment, at 0.57 relative to length of tarsus (Fig. 39), interval between basal seta and base of tarsus 1.3 times that of height of tarsus, distance from basal seta to dorsal fossary seta 20–22 µm. All tarsi with pair of parambulacral setae and pair of claws.

Male unknown.

Remarks. In the females, the number and shape of the ventral setae on tibia IV proved to vary from two to four. The apical pair of setae always is present, the two mid-segmental setae, one bipectinate, one slender, may be lacking on either one or both legs. Unilateral differences are very common. In ten females studied the most common combination of setae on tibia IV was, presence of the slender ventral mid-segmental seta but absence of the pectinate seta (11 legs, 55 %). On five tibiae IV (25 %) both a pectinate and a slender mid-segmental seta were present, whereas on three tibiae (15 %) both mid-segmental setae were absent. A single tibia IV (5 %) had a pectinate but no slender mid-segmental seta. In material (53 females) from North America (unpublished data), the presence of three ventral setae on tibia IV was the most common state (63 %), without any concentration on the one or other variant in a given locality (population). The four females collected on Hokkaido, Japan, had three ventral setae on tibiae IV, all pectinate (ABÉ 1990).

All instars have a small dorsolateral papilla on tarsus I (cf. Fig. 37), although in dorsomedial aspect the papilla may be obscured. ABÉ (1990) emphasized the similarity with a chemosensory organ. There is a very delicate afferent canal through the integument, so this papilla is not merely a part of the reticulum that covers the surface; it may represent a famulus.

3. 5. Development

The larva has a short idiosoma with three pairs of five-segmented legs. The dorsal plates AD, OC and PD are present, the PD is short (relative to length of the AD), the ornamentation of the plates is weak. The larva already has the final number of dorsal idiosomatic setae and gland pores. The AE has a pair of epimeral pores and two pairs of setae. The PE is short and bears a single seta. The anal sclerites are partly visible in dorsal aspect. The gnathosoma is characterized by its slender palps and rostrum.

In the protonymphs the epimeral plate IV and leg IV have been added. The OC and PD have increased in size, the OC in the medial and posterior portion, the PD both anterior to the pair of ds-4 and between the gland pores. The PE that now includes epimeral plate IV is much longer than in the larva but the PE still bears a single seta. On the AE a pair of setae on epimeral plate II has been added. The epimeral pores are still present though less conspicuous than in the larva. A genital plate, fused with the anal plate, and a pair of genital acetabula have been added. The shape of the gnathosoma resembles that of the larva but the position of the seta on P-2 has changed in this and the following instars. The femora of the three larval pairs of legs are divided, hence the legs are six-segmented, leg IV is five-segmented. The tibiae have increased in length, relative to the tarsi. Setae have been added to the basifemora I to III, telofemur III and genua I and II.

The deutonymph differs from the protonymph in that the epimeral pores of the AE are reduced, on the PE a short dorsal and long ventral seta are added and the GA bears two pairs of genital acetabula and two pairs of pgs. Both pairs of setae are anterior to the genital acetabula. All legs are six-segmented. Changes in the number of setae are summarized in Table. 4. Setae have been added on basifemur IV, telofemora I, II and IV, and genua and tibiae I to III.

In the female both the dorsal and ventral plates are longer and wider and their reticulate ornamentation is much more prominent than in the nymphs, and the areas of striated integument between the plates are narrow. On the large GA a posterior pair of pgs has been added and in the middle of the plate is the large genital opening. Two pairs of genital acetabula have moved onto the genital sclerites, a third pair is on the inner flank of the sclerites. The anal sclerites are in a ventral position. The shape, number of setae and the ratio of gnathosoma to idiosoma is similar to that of the other instars, P-2 has grown in length and the seta, in almost mid-segmental position in the larva, is now in an apical position. All legs, especially their tibiae, have increased in length; tibia I is 1.7 times longer than tarsus I (instead of 1.1–1.2 times as in the larva). The tarsi are more slender (length:height ratio) than in the larva, extended in length primarily at their bases, as demonstrated on tarsus III. The basal seta of tarsus III is positioned at 0.56 in the female, but at 0.46, 0.38 and 0.27 in the preceding instars, respectively. The setation of the tibiae often differs from that in the deutonymph, that of the other leg segments is the same in both instars.

The number of setae on trochanters and tarsi is unchanged throughout all instars.

4. BIOLOGY AND DISTRIBUTION

The majority of records of *Porolohmannella violacea* are from standing surface waters, swamps, ponds and lakes, though the species also has been extracted from the groundwater (GLEDHILL, 1973, 1982; STRAYER, 1988). *Porolohmannella violacea* inhabits altitudes from the sea level (coastal waters) to mountain lakes in almost 2000 m, e.g., the Lacs de Estibère in the Pyrenees (ANGELIER 1965) and the Statzer See in the Alps (WALTER 1922), and a variety of substrata, sand, flocculent ooze, vascular plants, mosses, algae and also gill chambers of crayfish. Details on the life cycle are not known, other than that females are ovigerous most time of the year, carrying one to six eggs each. The presence of a large number of larvae in spring 2006 (beginning of June), as well as deutonymphs and females, and the appearance of protonymphs in the sample from July, seems to be an evidence for intense reproduction in spring.

All present records are from the northern hemisphere (Fig. 40), from Europe, Greenland, North America, and Japan (K. VIETS 1956; K.O. VIETS 1978, 1987; GREEN & MACQUITTY, 1987; PE≠IC 2004; BARTSCH 2006). The data summarized in Fig. 40 include unpublished records from Spain, Portugal and Canada (Northwest Territories, British Columbia, Alberta, Manitoba, Ontario, Quebec, Newfoundland). Several of the collecting sites (e.g., in Greenland and Northwest Territories (lake near Tuktuyaktuk)) are ice-covered for most of the year. In contrast, the small pond near Hamburg, hardly shaded by trees, was exposed for several weeks to unusual long-term solar radiation, high temperatures and deteriorating oxygen supply. The pond was rapidly evaporating in July. Beneath a cover of dried remnants of a former vegetation, in a moist mixture of sediment, debris and mosses, specimens of *P. violacea* still were alive. At a visit to the pond at the end of August, after repeatedly heavy rainfall and distinctly lowered temperature, the moss was found to be regenerating. In the sample examined *Porohalacarus alpinus* and *Hydrozetes* sp. were still present in moderate numbers, adults as well as juveniles. The number of specimens of *Porolohmannella violacea* had decreased considerably, but still, larvae, nymphs and females were found.

5. DISCUSSION

In several descriptions of the freshwater halacarids *Lobohalacarus weberi*, *Porohalacarus alpinus*, *Soldanellonyx monardi* and *S. chappuisi* Walter, 1917, the external characters of the one or other juvenile have been briefly outlined (WALTER 1919b; WALTER & BADER 1952; BARTSCH 1973, 1975, 1982); unfortunately some species are described exclusively on the basis of nymphs (WALTER 1919a; VIETS 1931; JANKOVSKAJA 1967). Now, the development of external characters from larva to adult of *Porolohmannella* has been examined. The marine genera best studied in respect to their development are *Copidognathus*, *Isobactrus*, *Rhombognathides* Viets, 1927, *Metarhombognathus* Newell, 1947 and *Rhombognathus* Trouessart, 1888 (BARTSCH 1998, 2003).

In contrast to many other aquatic mite taxa, e.g., Hydrachnidia and Oribatida, the juvenile instars of halacarid mites do not differ markedly from adults, though of course they are of smaller size. Halacarids have no apparent change in habitat or life-style.

Freshwater halacarids progress through one larval and two nymphal instars until they moult into the adult. A single exception, *Astacopsiphagus parasiticus* Viets, 1931, a mite found on freshwater crayfish in Australia, has three nymphal instars in its life cycle (VIETS 1931). Marine halacarids have one to three nymphal instars.

The character development in *P. violacea* is similar to that known in other halacarid species (cf. BARTSCH 1998, 2003). Minor differences are:

(a) In *P. violacea* epimeral pores are present in the larva but also in the protonymph; they are absent in the deutonymph and female. In most marine species in which adults lack epimeral pores, these pores are restricted to the larva.

(b) There is a striking change in the length ratio of tibia to tarsus, with a marked growth of the tibiae compared with that of the tarsi. Such a difference in length has not been described before. Adults of *P. violacea* are long-legged, but marine species studied so far are short-legged. Long-legged marine species may show a similar shift in the length relation.

(c) From instar to instar, the basal seta on tarsus III and the seta on P-2 are moved to a more apical position. The segments obviously grow in length near their bases. In marine genera, a similar but much less marked growth near the base of the tarsi has been documented. The marine species studied to date are short-legged whereas the nymphs and females of *P. violacea* have long and slender legs and palps.

Karl VIETS (1927, 1933) once distinguished between halacarid species of marine and freshwater, between Halacaridae and Porohalacaridae, respectively. That distinction has been abandoned (NEWELL 1947, 1959; BARTSCH 1973, 1989; PETROVA 1974, 1981) because it was not supported by synapomorphies. The ontogeny of *Porolohmannella violacea* is similar to the development of characters in marine halacarid species, and hence does not support a taxonomic separation into marine and freshwater families.

According to Fig. 40, *P. violacea* is wide-spread throughout the northern hemisphere. These data do not imply that *P. violacea* is restricted to the holarctic. *Porolohmannella violacea* is euryvalent and thrives in a variety of habitats, in standing as well as in running water, in brackish coastal as well as humic inland waters, it can withstand long-term solar radiation with rising water temperature, but also ice-covering for more than six months. One may speculate that high temperature prevents a colonization of the tropics, but the *P. violacea* population in northern Germany proved to withstand the hot summer in 2006. Hence, the temperature in the tropics should not hamper a distribution. According to TESCHNER (1963) and SIEMER (1996), in the freshwater halacarid *Lobohalacarus weberi* and the marine *Metarhombognathus armatus* (Lohmann, 1893) a cold season is needed in the course of development. Does the higher and more uniform annual temperature cycle in warm-temperate and tropic areas prevent *P. violacea* from colonization? Presumably not. *Lobohalacarus weberi* has been collected in the southern hemisphere, in Australia (Queensland, near Brisbane) (unpublished), in an area with an annual surface water temperature range between 16 °C and 29 °C (DAVIE 2004). Similarly, *P. violacea* may thrive in the tropics and southern hemisphere. The present geographic distribution, restricted to the holarctic, is merely the result of the extraordinarily low number of samples taken in the south compared to that in the north. *Porolohmannella violacea* may be Mesozoic, or even Pre-Mesozoic, in origin (BARTSCH 1996). The species is expected to be found in South America, Africa and Australia, either being a remnant of a Pangaean fauna or introduced by means of birds, mammals, insects, extreme floods and storms.

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Patterns of Geographic Variation in Body Measures and Plumage Colour of the Brimstone Canary *Crithagra sulphurata* (Aves: Fringilidae)

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Abstract. The Brimstone Canary is a geographical highly variable species, distributed throughout southern and eastern Africa. Here I present data on body measures and plumage characteristics of 476 skins from all parts of the species' range (Fig. 1). In both univariate and multivariate analyses the wing and beak measures showed the most remarked differences between populations (Tab. 2, 5). Variation parallels climatic trends with individuals from hot and humid regions have shorter wings and smaller beaks (Tab. 7). In contrast to earlier studies plumage colour should not be used to distinguish populations, because of high individual variation (Tab. 8).

Only skins from South Africa (including Natal and Zululand) could be separated clearly (stronger beaks) from all other populations (shorter wings, less strong beaks). Clinal variation and high individual variation did not allow more differentiation in the northern part of the range. Therefore, the data are in agreement with the separation of the subspecies *sulphurata* (in South Africa) and sharpei (all other populations), while *wilsoni* and all other subspecies are not supported.

Keywords. Multivariate analysis, subspecies, wing dimensions, beak size, individual variation.

1. INTRODUCTION

The traditional way to describe spatial variation of species is the recognition of subspecies. Subspecies are more or less clearly separated from other populations of the same species by differences in at least one trait and are distributed in a more or less clearly defined subarea of the species' range. This method gives, however, an incomplete picture of variation, because many traits vary in clines and the spatial characteristics of clines may differ from trait to trait (see GOULD & JOHNSTON 1972 and ZINK & REMSEN 1986 for reviews).

Hence, to distinguish a representative of a subspecies from an individual variant or a local form in a cline profound knowledge of individual and geographical variation within the species is necessary. Such knowledge was not available when most subspecies have been described and is still not available for many species.

The Brimstone Canary *Crithagra sulphurata* is such a geographical highly variable species. Within the Canaries five afrotropical species form the monophyletic genus *Crithagra* as suggested by morphological, ethological and molecular data (van den ELZEN 2000). *C. sulphurata* inhabits grasslands and savannas with scattered trees throughout southern and eastern Africa (Fig. 1). Within this range and especially in its eastern part a high degree of morphological variation has led to the description of seven subspecies:

- *sulphurata* (Linnaeus, 1766) (LINNAEUS 1766, Syst. Nat., ed. 12,1: 305), type from Cape of Good Hope,
- *sharpii* (Neumann, 1900) (NEUMANN 1900, J. Ornithol. 48: 287), t.t. Marangu, Kilimanjaro,
- *shelleyi* (Neumann, 1903) (NEUMANN 1903, Ornithol. Mber. 11: 184), t.t. Kafuro, NW Tanzania,
- *frommi* (Kothe, 1911) (KOTHE 1911, Ornithol. Mber. 19: 71), t.t. Namanjera, Ufipa, SW Tanzania,
- *loveridgei* (van Someren, 1921) (van SOMEREN 1921, Bull. Br. Ornithol. Club 41: 114), Lumbo, northern Mozambique,
- *wilsoni* Roberts, 1936 (ROBERTS 1936, Ann. Transv. Mus. 18: 216), t.t. Kloof, Natal, and
- *languens* Clancey, 1962 (CLANCEY 1962, Durban Mus. Nov. 6: 193), type from Manhica, Sul do Sava, southern Mozambique.

Different authors have adopted controversial positions which of these types represent real subspecies, e.g., FRY & KEITH (2004) in their recent review recognized only three of these *(sulphurata, sharpei, wilsoni)*. RAND (1968) and CLANCEY (1972) reviewed available measurements and distribution data and concluded, in accordance, that most of the "subspecies" mentioned above are not sharply separated from each other in the traits considered. Due to larger body size and stronger beaks South African nominate *sulphurata* can be distinguished from all other forms with relative ease. Therefore, Rand accepted only two subspecies: *sulphurata* and *sharpei* (all populations except South Africa). In an alternative view he divided *sharpei* on the basis of subtle differences in plumage colour and size into four subspecies: *wilsoni* (Natal, southern Mocambique), *sharpei* (Kenya), *frommi* (Tanzania, Zambia and Angola) and *shelleyi* (all other populations). In contrast, Clancey (1972) separated four subspecies in South Africa alone *(sulphurata, wilsoni, languens* and *shelleyi).* Both studies are, however, based on only a few traits and from some regions only a small number of individuals have been included.

In this study I present data on a larger variety of measures and plumage characteristics of *C. sulphurata* skins from all parts of the species' range. The aim of this study is to describe the extent and pattern of geographic variation in this species. Which of the subspecies described earlier represent real taxonomic units and which are intermediate stages arbitrarily picked out of a continuous cline of variation? In a second step I want to relate morphological variation to possible causal factors such as ecological conditions (climate, vegetation, topography) and palaeographic events.

2. MATERIAL AND METHODS

I measured a total of 485 museum skins of *Crithagra sulphurata,* of which all 476 adults (253 males, 171 females and 52 unsexed) were considered in the following analyses. Additionally, I studied 24 skins of the sister species (van den Elzen 2000), *Crithagra flaviventris*, for comparison (15 males, 9 females). The skins are kept by Zoologisches Forschungsmuseum Koenig (ZFMK), Bonn, Zoologisches Institut und Museum (ZMH), Hamburg, Zoologisk Museum (ZMUC), Copenhagen, Zoologische Staatssammlung (ZSM), Munich, Natural History Museum (BMNH), Bird Group, Tring, and Royal Museum of Central Africa (RMCA), Tervuren, respectively.

Tarsus and beak measures (length, width and height in both cases) were taken from all specimens. Length of wing, tail and first to ninth primaries as well as Kipp's distance (wing tip to first secondary) and graduation of tail were measured in all except molting specimens. From the wing measures I calculated Wing Pointedness Index I and II after Mlikovsky (1978) and Hedenström (1989), respectively. Plumage colours (throat, breast, belly and back) were compared with standardized colour maps (Scandinavian Colour Institute 2001). For statistical analysis I described standard colours by four variables: proportion of black, of colour, green (negatively correlated to proportion of yellow due to construction of the colour system), and red *(C. flaviventris* only). Not all traits could be taken for all individuals because of skin condition. Therefore, sample sizes differ from analysis to analysis.

Skins with geographical origin close to each other have been pooled for analysis, resulting in 15 'populations' (Fig. 1). Individuals which locality information were lacking, unclear or doubtful (e.g. Collection Meinertzhagen; *cf.* Knox 1993) were included in the analyses, but considered as belonging to none of the populations. To get larger sample sizes some of the populations were pooled to larger 'population groups' (A–G) in some analyses (Fig. 1).

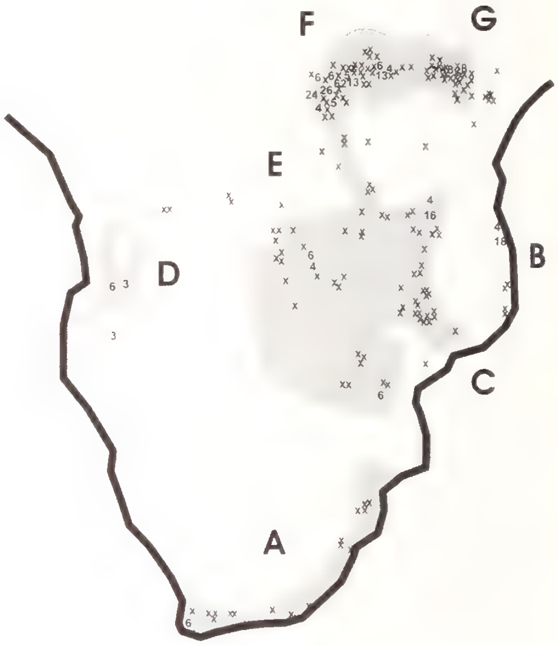

Fig. 1. Map of collection localities of skins (crosses - single skins; numbers - series with number of collected individuals). Ellipses define "populations". "Population groups" are marked by letters A to G. The present breeding distribution of *C. sulphurata* (simplified after Fry & Keith 2004) is shaded.

Predominant vegetation structure was revealed for each skin locality using the vegetation map of EC-JRC (2003, map 2) summarizing all categories under 'dominant tree layer' as 'forest' and all categories under 'dominant agriculture' and 'dominant shrub or grass layer' as 'open habitat'. Climatic data of the closest weather station were taken from Lebedev (1970). Because of the scarcity of weather stations, up to 63 skins gathered on one weather station and, in these cases, I used the mean for each trait. The following data were considered: yearly mean of mean, maximum, minimum and range of air temperature per day, yearly sum of precipitation, daily maximum of precipitation. Altitudinal effects could not be taken into account because for most skins altitudinal information were not available with sufficient accuracy.

Non-parametric Factor Analysis were performed using the MS Excel Add-In XLSTAT 7.0 (Addinsoft 2003). For all other calculations I used the software package SPSS for Windows 11.0 (SPSS 2001).

3. RESULTS

3.1. Data preparation

Some variables were transformed to fit a normal distribution: beak height (reciprocal square root transformation), first primary length (reciprocal), graduation of tail (natural logarithmic) and the tarsus measures (cube). All other metric variables did not differ significantly from normal (Kolmogorov-Smirnov One-sample-test, p>0.05).

The plumage colour variables have been subjected to a non-parametric Factor Analysis based on Spearman's rank correlation. After Varimax rotation the resulting three factors with eigenvalues larger than 1 explain 88 % of the variance (Tab. 1). The first factor (hereafter called 'front colour' or 'C1') is highly associated with belly and throat colour; higher values represent individuals with more yellowish and less greenish front plumage. C2 ('back colour') describes back colour, higher values correspond with more black and less colour components in the back plumage. The colour of the breast is highly correlated with C3 ('breast colour'). Individuals with high values of C3 have darker and more greenish breasts while low C3 values indicate yellowish breasts. For further analysis I used the factor scores of C1–C3 for each skin.

Table 1. Correlations between plumage colour variables and factor scores from a Factor Analysis based on a Spearman's rank correlation matrix. Correlations > 0.6 printed bold.

Factor	C1	C2	C3
belly: % black	-0.367	0.226	0.027
belly: % colour	**0.751**	-0.053	-0.134
belly: % green	**-0.740**	0.045	0.175
breast: % black	-0.056	0.248	**0.943**
breast: % colour	0.336	-0.223	**-0.747**
breast: % green	-0.225	0.010	**0.620**
back: % black	-0.147	**0.717**	0.332
back: % colour	0.243	**-0.951**	-0.188
back: % green	-0.141	-0.307	0.026
throat: % black	-0.567	0.160	0.119
throat: % colour	**0.723**	0.002	-0.145
throat: % green	**-0.776**	0.015	0.248
eigenvalue	4.4	1.6	1.1
% variance explained	38.7	22.3	27.8

3.2. Morphological differences between *C. sulphurata* and *C. flaviventris*

At first I looked at differences in morphological characteristics between *C. sulphurata* and its sister species, *C. flaviventris*. A Discriminant Function Analysis (DFA) reduces the 21 morphological variables to a single canonical variable with an eigenvalue of 1.13 and a canonical correlation of 73 %. Two beak measures and two wing measures are included in the analysis (standardized canonical coefficients in parenthesis): beak length (1.533), beak height (0.696), 1st primary length (0.463) and distance from wing tip to secondaries (0.343). Values for *C. flaviventris* are lower, thus, skins of this species are smaller in beak and wing dimensions. 95 % of all skins have been classified correctly by the DFA. An additional trait for differentiation is a red component in the front plumage of *C. flaviventris:* 13 of 21skins had a slight tinge of red, but none of the *C. sulphurata* skins.

3.3. Differentiation of *C. sulphurata* populations

Most traits differ significantly between populations (Tab. 2). Wing and beak measures show high levels of differentiation (high significance values) in both males and females. For a detailed analysis I tested for each trait if there is a difference between population groups. Again, the most pronounced differences are in the wing and beak measures (Tab. 3). Of 21 population group pairings 16 (males) and 11 (females) differ significantly in at least one wing measure, respectively, and 12 (males) and 6 (females) in at least one beak measure, respectively. The populations of Kenya (group G) and South Africa (A) are separated by differences in most traits from all other population groups, but not from each other. In the central part of the species' range populations vary hardly. There is a tendency for females to differ in fewer traits than males across the same population group pairings.

Many of the studied traits correlate with each other (e.g. wing length and primary length). Intercorrelations may occur between all variables. Therefore, I performed a Principal Component Analysis (PCA) on all 24 original meas-

Table 2. Univariate differences in *C. sulphurata* traits between populations (one-way ANOVA). *significant differences on the 5%-level (corrected for 24 tests: P<0.05/24=0.0021).

	males			females		
	df	F	Sig.	df	F	Sig.
wing measures						
wing length	13/215	19.002	0.000*	13/146	10.548	0.000*
1st primary length	13/192	8.443	0.000*	11/127	4.040	0.000*
2nd primary length	13/192	7.286	0.000*	11/128	4.660	0.000*
3rd primary length	13/197	7.083	0.000*	11/129	6.708	0.000*
4th primary length	13/189	7.733	0.000*	11/124	4.818	0.000*
5th primary length	13/195	11.383	0.000*	11/129	6.202	0.000*
6th primary length	13/194	15.328	0.000*	11/131	11.721	0.000*
7th primary length	13/195	19.416	0.000*	11/132	11.504	0.000*
8th primary length	13/188	17.909	0.000*	11/131	10.368	0.000*
9th primary length	13/191	12.721	0.000*	11/130	7.282	0.000*
Kipp	13/213	2.797	0.001*	13/142	1.433	0.151
wing index I	9/61	0.534	0.844	9/39	1.242	0.299
wing index II	9/61	0.494	0.873	9/39	1.082	0.397
tail measures						
length	13/216	7.475	0.000*	13/145	5.812	0.000*
graduation	13/214	1.230	0.259	13/143	1.025	0.431
beak measures						
length	13/217	9.009	0.000*	13/147	7.826	0.000*
height	12/104	11.610	0.000*	13/73	9.792	0.000*
width	13/218	20.355	0.000*	12/146	12.610	0.000*
tarsus measures						
length	13/216	4.631	0.000*	13/147	5.756	0.000*
width	13/215	2.576	0.002	13/147	2.681	0.002
height	13/215	2.650	0.002	13/147	3.632	0.000*
Plumage colour						
front colour	13/218	3.169	0.000*	13/147	1.487	0.129
back colour	13/218	4.592	0.000*	13/147	2.047	0.021
breast colour	13/218	4.067	0.000*	13/147	3.862	0.000*

ures (21 morphometric and 3 colour traits). It reduces the data set to five uncorrelated factors that together explain 65 % of the variance (Tab. 4). The correlations between the first factor (PC1) and length of wing, tail and all primaries are all relatively large and positive (1st primary appears inverse due to transformation). It can be taken as a multivariate measure of size; individuals with high PC1 values are larger in size. The second factor summarizes the three beak measures: higher PC2 values indicate individuals with stronger beaks (beak height transformed as 1st primary). PC3 and PC4 represent wing shape and breast colour, respectively. The fifth factor correlates negatively with front plumage and positively with back plumage. Individuals with high PC5 scores are, therefore, darker on their back and more greenish on their front, while individuals with low PC5 scores are more greenish on their back and more yellowish on their front.

Table 3. Differentiation of traits (raw measures) between the population groups A to G. Shown are traits with significant differences on the 5%-level (Mann-Whitney-U-test, significance level corrected for 24 tests as in Tab. 2). The diagonal separates male (right) and female (left) analyses.

Abbreviations: l – length, w – width, h – height; 1–9 first to ninth primary length. B, C, G: proportion of black, colour and green of breast, throat, belly and back plumage, respectively.

	A	B	C	D	E	F	G
A		wing: l, Kipp, 1-9 beak: l, h, w tail l breast: BC	wing: l, Kipp, 1-9 beak: l, h, w tail l	wing: 1,2, 8 beak: l, w	wing: l, 1, 3, 6 beak: l, h, w tail l	wing: l, Kipp, 1-9 tarsus: w, h beak: l, w tail l belly: CG breast: BC throat: G	beak: h, w
B	wing: l tarsus: l beak: l		wing: l, 1-9	wing: 2, 4, 5	wing: l, 1-9 tarsus: l tail l back: G	wing: l, 1-9 beak: w throat: G	wing: l, 1-9 tarsus: l beak: l, w tail l back: G
C	Schn: L						wing: l, 1-9 Schn: L , H , Br
D	wing: l beak: l tail l				wing: 8		wing: l, 2, 7, 8 beak: l
E	beak: l, h, w	wing: l, Kipp, 2, 4-9		wing: l, 4-9		wing: l, 2, 5-9 tarsus: l tail l belly: G breast: C back: BC	wing: l, 1, 3-9 beak: l, h, w
F	wing: l tarsus: l beak: l, h, w tail l breast: BC	wing: 7			wing: l, 1-9 tail l breast: BC back. BC		wing: l, 1-9 tarsus: l, w beak: l, h, w tail l
G		wing: l, Kipp, 2, 7-9 tarsus: l beak: l		wing: l	wing: 7	wing. l, 2, 3, 6-9	

Table 4. Correlations between the 24 original measures and principal component scores from a PCA (using Varimax rotation with Kaiser normalization) of the correlation matrix of 476 *C. sulphurata* skins. Correlations >0.600 are printed bold.

Variable	PC1	PC2	PC3	PC4	PC5
wing length	**0.864**	0.331	0.137	0.105	0.013
1st primary length	**-0.726**	-0.171	0.199	-0.108	-0.156
2nd primary length	**0.780**	0.124	-0.274	0.087	0.173
3rd primary length	**0.800**	0.120	-0.292	0.029	0.120
4th primary length	**0.822**	0.077	-0.298	-0.013	0.059
5th primary length	**0.858**	0.119	-0.236	0.039	0.011
6th primary length	**0.891**	0.208	-0.012	0.103	0.022
7th primary length	**0.919**	0.215	0.091	0.100	0.040
8th primary length	**0.905**	0.224	0.141	0.092	0.050
9th primary length	**0.844**	0.203	0.137	0.100	0.102
Kipp distance	0.366	0.198	0.234	0.036	-0.208
wing index I	-0.111	-0.029	**0.946**	0.037	0.041
wing index II	-0.110	-0.012	**0.943**	0.038	0.007
tail length	**0.636**	0.273	0.081	0.125	0.105
tail graduation	0.012	0.182	-0.035	0.461	-0.082
tarsus length	0.286	0.048	0.052	0.625	0.189
tarsus width	0.094	0.369	-0.015	0.106	0.296
tarsus height	0.181	0.294	0.004	0.209	0.319
beak length	0.400	**0.697**	-0.010	0.148	-0.009
beak height	-0.218	**-0.823**	0.033	-0.020	-0.023
beak width	0.382	**0.729**	-0.004	0.078	0.096
front colour	0.032	-0.153	0.027	0.133	**-0.661**
back colour	0.170	-0.055	0.050	0.009	**0.683**
breast colour	0.036	-0.011	0.071	**0.810**	-0.081
eigenvalues	8.172	2.463	2.270	1.452	1.296
% variance explained	34.0	10.3	9.5	6.1	5.4

Table 5. Standardized Canonical Discriminant Function Coefficients from a DFA of the five PCA scores of 443 *C. sulphurata* skins from the population groups A to G.

PCA-factor	DF1	DF2	DF3	DF4
PC1	**0.824**	**-0.633**	-0.272	-0.007
PC2	**0.816**	**0.612**	-0.32	-0.184
PC4	0.52	-0.026	**0.779**	-0.455
PC5	0.516	0.178	0.365	**0.809**
eigenvalues	1.517	0.244	0.136	0.015
% variance explained	79.3	12.7	7.1	0.8
canonical correlation	0.776	0.443	0.346	0.122

Table 6. Proportion (%) of skins classified correctly as belonging to population group A–G by the DFA. N - sample size.

	N	A	B	C	D	E	F	G
A	29	**79**	0	0	0	3	3	14
B	27	0	**0**	0	0	0	100	0
C	36	0	0	**0**	0	8	89	3
D	14	0	0	0	**0**	21	79	0
E	72	3	0	0	0	**40**	53	4
F	231	1	0	1	0	3	**94**	1
G	34	9	0	0	0	18	21	**53**

To determine which of these factors have the highest selectivity for the population groups, I performed a stepwise Discriminant Function Analysis (DFA) on the PCA scores (Tab. 5). PC3 (wing shape) does not contribute to differentiation between groups and is removed by the analysis. The other four PCA scores are transformed to four DFA factors. 65 % of skins are classified correctly by this analysis. There are, however, marked differences between the population groups in the proportion of correct classification (Tab. 6). Population group A (South Africa) is clearly divided off from all other groups. Population group G (Kenya) is separated less, but more than 50 % of skins are classified correctly. Most overlapping of G-skins is with group A. Nearly all other skins from groups B, C, D, E and F are classified as belonging to population group E (Congo, SW Tanzania) or F (Kivu/Uganda/Rwanda). Separating males and females in a single DFA each gives similar results and is, therefore, not presented here.

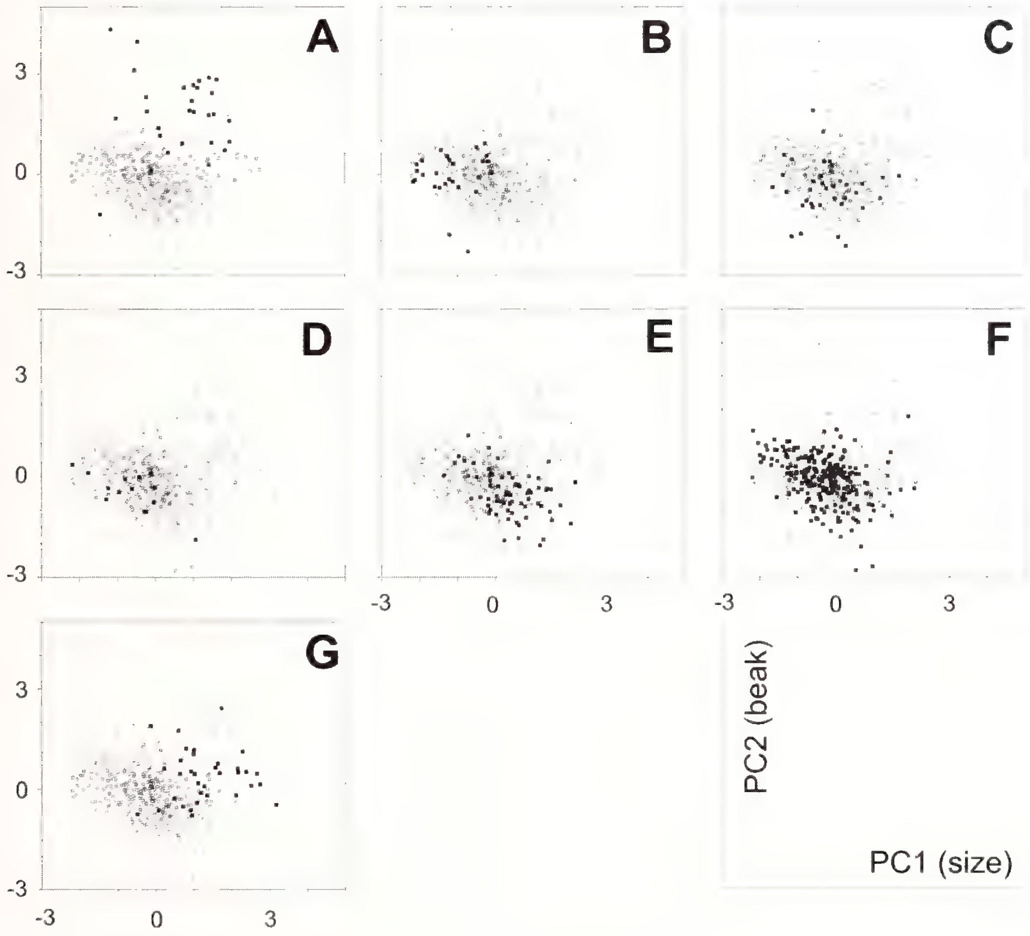

Fig. 2. *Crithagra sulphurata* skins in the space defined by principal components 1 and 2 (see Table 4). Solid symbols - all skins; filled symbols - skins from population group A to G, respectively.

The groups B to F of eastern Africa which appear homogenous in the above population group analysis may be differentiated on a lower level. Therefore, I calculated a DFA at population level on all skins except from population group A and G. Again, most skins are classified as belonging to populations of group E or F.

3.4. Pattern of geographic variation

The large range of classification accuracy by DFA (Tab. 6) indicates that some population groups are more separated from their neighbours than others. Scores of all groups overlap to some extend with the characteristics of other populations (Fig. 2). The pattern of variation is much more complex than described by clear-cut population groups. As an example, in Fig. 3 / Fig. 4 wing length and beak width are shown against the geographical origin of the skins.

The population group with lowest overlap to other groups is South Africa (including Natal; group A). South African *C. sulphurata* are characterized by strong beaks and large to intermediate body sizes (Fig. 2). Within population group A both wing and beak measures are relatively homogeneous (Fig. 3, Fig. 4). Skins from Natal have a little bit lower scores in both principal components, thus distinguished by little weaker beaks and little shorter wings/tails. The differences to the next population in the north (group C) are, however, much more remarkable than the differences between the South African and Natal population (Figs 2–4).

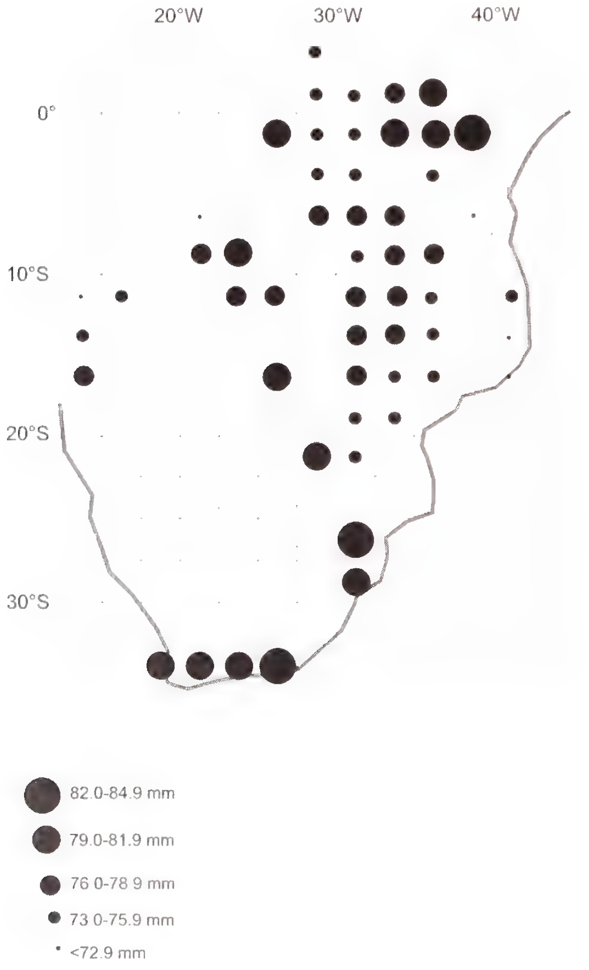

Fig. 3. Variation of wing length of *C. sulphurata*. Shown are means for 2°30'-fields with at least one studied skin. The solid line schematizes the coastline of southern and eastern Africa.

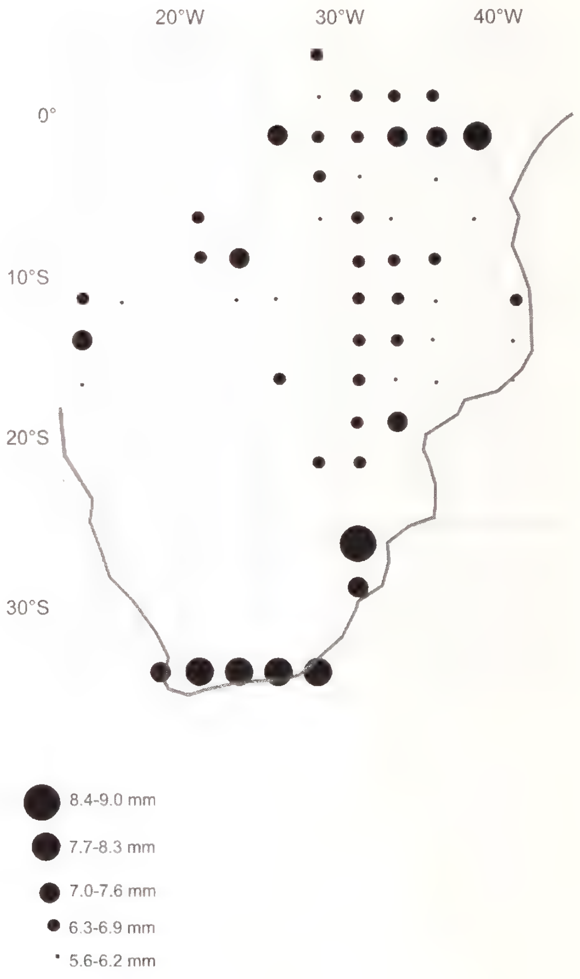

Fig. 4. Variation of beak length of *C. sulphurata*. See Figure 3 for explanation.

In relation to all other groups Kenyan *C. sulphurata* (group G) look similar to skins from the other end of the species' range, group A. Beaks of skins from Kenya are intermediate between South African birds and all other groups, while body size is larger in Kenya than in all other groups (Fig. 2). Overlap to neighbouring populations is, however, considerable. As shown by Fig. 3 and Fig. 4 the population of Kenya is less homogenous in both beak and wing measures. Skins from northern Kenya have as long wings as skins from southern Kenya, but in respect to beak size they resemble birds from the eastern and central part of the species' range.

Outside Kenya and South Africa no remarkable morphometric differentiation between population groups exist. There is a tendency, however, for skins from Mocambique (B) and Angola (D) to be smallest in both principal components (Fig. 2). Wing length increases from the coasts to central Africa and could be described as a quadratic function of geographic longitude ($WING=-1.23E-10*LONG^2 + 6.87E-05*LONG + 66.25$; $R^2=0.06$; ANOVA df=2/374 F=11.1 P=0.000). Beak width variation is clinal, too, and fits a linear function with highest values at the eastern coast ($BEAK=-1.51E-06*LONG+6.82$; $R^2=0.03$; ANOVA df=1/376 F=11.2 P=0.001). Apart from this clear trend, for both measures areas with low scores alternate with high score areas, however (Fig. 3, Fig. 4).

The clinal longitudinal trend is visible in the PC1/PC2 plot as a shift along the axis B (Mozambique) to C (Malawi/Zimbabwe) to E (Congo/Tanzania; Fig. 2). Due to high intra-group variability both population group F (Kivu/Rwanda/Uganda) and D (Angola) overlap with nearly all other central population groups. Skins from these two groups are, therefore, indistinguishable from the other population groups except A and G. Hence, the DFA could not dissolve the population groups B to F (Tab. 6) and classified all skins from the central part of the species' range as belonging to group F.

3.5. Impact of climate and vegetation

To reveal associations between variation of morphological traits of *C. sulphurata* and climatic conditions I performed a PCA with the six climatic variables mentioned above and the five principal components of morphological measures *(cf.* Tab. 4). The resulting two factors explain 45 % of total variance (Tab. 7). The first principal component (cPC1) shows that body size (PC1) decreases along a gradient of increasing temperature. Large *C. sulphurata* can be found under relatively moderate temperature conditions. Beak dimensions decrease as sum of precipitation increase. Therefore, strong beaks are associated with relatively dry climate.

Table 7. Correlations between the 6 climatic variables, the 5 principal components (cf. Table 4; mean for each weather station) and principal component scores from a PCA (using Varimax rotation with Kaiser normalization) of the correlation matrix of 68 weather stations. Correlations >0.6 are printed bold.

variable	cPC1	cPC2
mean of temperature	**0.898**	-0.240
maximum of temperature	**0.850**	-0.146
minimum of temperature	**0.916**	-0.089
range of temperature	-0.262	-0.057
sum of precipitation	-0.041	**-0.801**
maximum of precipitation	-0.468	-0.064
PC1	**-0.641**	0.443
PC2	0.149	**0.785**
PC3	-0.156	0.016
PC4	-0.089	0.327
PC5	-0.238	0.329
eigenvalues	3.4	1.5
% variance explained	31.0	13.9

Table 8. Mean variance of principal components (see Tab. 4) at eight localities ("local"; between 8 and 15 skins, total N=59) and in a random sample of the respective populations ("population"; same sample sizes). "Significant": number of the eight local-population pairings with significant differences in variance (Levene's test, p<0.05).

Component	Local	Population	Significant
PC1 (body size)	0.59	0.93	2
PC2 (beak size)	0.48	0.79	1
PC3 (wing shape)	1.03	0.53	1
PC4 (breast plumage)	0.77	1.19	1
PC5 (front/back plumage)	0.80	1.44	1

Skins from forested areas have lower scores of the size-related first principal component (thus, are smaller in size; mean -0.12) than skins from open landscape (mean 0.07; t-test t=2.06 *df*=416 P=0.040; P all other PC >0.05). This difference is more pronounced in Kenyan skins (population group G), where it is highly significant (t=3.76 *df*=32 P=0.001).

3.6. Individual variation

From seven localities I have series of eight or more skins that had been sampled in the same season (within three month). I compared variability of these samples with variability in a random sample of same sample size taken from the same population. In principle variances of local samples are slightly smaller than population variances (Tab. 8), but this difference is significant in only one or two of eight pairings. Mean variances of the eight samples are smaller in principal components 1 and 2 (body and beak size) than in the other variables (plumage colour). This is true for both local and population level samples.

4. DISCUSSION

The morphological variability of *C. sulphurata* is considerable. Differences in body dimensions and plumage colour occur not only between populations but also individually at a single locality (Tab. 8). Therefore, if geographical variation is studied attention has to be paid to individual variation, too.

In both univariate and multivariate analyses wing and beak measures show the most striking differences between populations (Tab. 2, 5) . Wing and beak measures also exhibit lowest individual variation at one locality (Tab. 8). Therefore, these traits are suitable to separate populations and subspecies. The revisions of RAND (1968) and CLANCEY (1972) were based on wing and beak measures, too. Additionally, both authors considered slight differences in plumage colouration (a little more greenish/yellowish etc.) to recognize subspecies. My study of a larger sample of skins shows, however, that plumage colour varies enormously at one site (Tab. 8) and can not be used to distinguish populations.

Morphological variation of *C. sulphurata* parallels climatic trends: individuals from hot and humid regions have shorter wings and smaller beaks (Tab. 7). The pattern of variation in wing and beak size (Fig. 3, Fig. 4) could be explained by altitudinal effects to a large extend. Similar climatic conditions may be responsible for similar trait dimensions of the populations of Kenya and South Africa, resident at the opposite borders of the species' range. Differences in body size in relation to predominate vegetation cover are probably a side-effect of climate, too, because also in rain forest areas *C. sulphurata* settles in the scattered open habitats and not in forests (FRY & KEITH 2004). Especially in Kenya, where *C. sulphurata* inhabits a broad range of altitudes, the relation between body size on one hand and climate and vegetation on the other hand is strong. In this population separation of sites close to each other but differing in altitude is obvious. If wing length is taken as a measure of body size, this climatic trend parallels Bergmann's rule, which suggest an increase of body size from cold to warm climates (ZINK & REMSEN 1986).

There is little evidence for geographical isolation of populations due to climatic changes in the past 20.000 years. Palaeovegetation records certify distinct changes in vegetation cover during this period (ADAMS 2004). Habitats occupied by *C. sulphurata* today (grasslands, scrub, savannas) have been driven back due to moister conditions during the holocene (about 10.000 years ago), resulting probably in a much smaller range of *C. sulphurata* at that time. However, open landscapes ranged continuously from southern Africa to Kenya, at the most interrupted by a narrow forest belt at 20–25° S.

Geographic variation reflects adaptation to different environmental conditions within a species' range. Therefore, it could be seen as a model of evolutionary steps of a single population over time in a changing environment (GOULD & JOHNSTON 1972). Differences in wing shape and size between populations often parallels migratory behaviour (LEISLER & WINKLER 1985). FRY & KEITH (2004) describe *C. sulphurata* as resident throughout its range. Short distance (altitudinal?) movements may occur in some populations, but at the most occasionally (MACKWORTH-PREAD & GRANT 1963, HARRISON et al. 1997). Therefore, morphological differences more probably reflect differences in habitat structure and use since body size and shape affect manoeuvrability (ZINK & REMSEN 1986). As LEISLER & WINKLER (1985) have shown in their comparative study, morphological characters are strongly correlated with foraging techniques. The variability of beak dimensions in this study suggests differences in foraging strategies or food composition of habitats within the range of *C. sulphurata*. In all parts of the range *C. sulphurata* settles in open habitats with scattered trees, food mainly consists of seeds and small fruits (MACKWORTH-PREAD & GRANT 1963, HARRISON et al. 1997, FRY & KEITH 2004). However, detailed information on geographic variation of habitat and food preferences is lacking. More field studies of the species are necessary to reveal this relationship.

Single traits can be linked due to developmental constraints. The PCA shows that the different measures of wing and tail size do not differ independently, but represent a single principal component (Tab. 4). This corresponds with many other studies, where the first, highly correlated factor could be interpreted as a size factor (GOULD & JOHNSTON 1972). The fact, that beak dimensions, wing shape and plumage colour each form separate factors, points to habitat or food related adaptations independent of size.

Only the skins from South Africa can be separated clearly from all other populations with the data presented here. The clinal nature of variation, the large overlap of trait measures and the large individual variation do not allow the recognition of subspecies in the remaining, northern part of the species' range.

C. sulphurata of the South African nominate subspecies *sulphurata* are characterized mainly by their strong beaks (Fig. 2). The range of this subspecies includes South Africa from the Cape Province to Natal and Zululand. In contrast, RAND (1968) recognized the population of the Cape Province as a separate subspecies, too, but classified the populations of north-eastern South Africa (Natal/Zululand) as belonging to another subspecies which includes all other populations in the north. Already MEES (1970) pointed to the fact, that the populations of the Cape Province and Natal are different from each other in plumage colour at the most, but not in other measures (see also RAND's own measurements). He therefore argued for combining both populations into one subspecies. The statistical analysis of skins presented here allows no separation between individuals from the Cape Province and Natal/Zululand, but separates between these and the populations in the north. These are isolated geographically, too, because *C. sulphurata* is lacking along the Limpopo River (HARRISON et al. 1997).

Individuals distributed in the northern part *(sharpei)* are – despite marked individual variation – smaller (shorter wings) and have less strong beaks than their South African congeners. Both traits vary outside South Africa in a complicated pattern without abrupt changes. Variation in both wing length and beak size have a clinal and an altitudinal compound. The separation of subspecies is arbitrarily and would not contribute to a better understanding of geographical variation in this case. At best the population of the Kenyan highlands could be recognized by relatively strong beaks, but the transition to neighbouring populations is fluid. A possible differentiation in traits not studied here (e.g., genetical or ethological) have to be reserved for future studies.

In conclusion, the data presented here are in agreement with the viewpoint of FRY & KEITH (2004) in respect to the subspecies *sulphurata* and *sharpei*, while the recognition of a subspecies *wilsoni* is not supported by this data set. A further differentiation of populations in the northern part of the range as done by other authors (see above) could not be confirmed in this study.

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A New Species of *Pseudachorutella* Stach, 1949 (Collembola: Neanuridae) from Poland

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Abstract. A new species of the genus *Pseudachorutella* Stach, 1949, *P. bescidica is* described from the Polish Carpathians. It is related to *P. assigillata* (Börner, 1901) and *P. balcanica* Cassagnau et Peja, 1978 described from Germany and Albania respectively. The new species is characterized by moderate plurichaetosis on dorsal side of the body, elongated labium, the presence of the male ventral organ and four teeth on claws.

Keywords. Entomology, taxonomy, Collembola, Neanuridae, *Pseudachorutella*, new species, Poland.

1. INTRODUCTION

The genus *Pseudachorutella* was established by Stach (1949) with *Pseudachorutes assigillatus* Börner, 1901 as the type species. Till now ten species have been described as *Pseudachorutella*, including four from Europe (Mari Mutt & Bellinger 1990; Massoud 1967; Najt & Weiner 1997; Najt et al. 1990; Weiner & Najt 1991). Morphologically, *Pseudachorutella* refers to *Arlesia* Handshin, 1942 (North and South America) and *Cephalachorutes* Bedos & Deharveng, 1991 (Asia, Africa). It differs from them by the set of subtle features in chaetotaxy of antennal segments III and IV (Bedos & Deharveng 1991). According to Deharveng (pers. comm.) it seems most probable that *Pseudachorutella* species occurring outside Europe belong to two mentioned genera or a new undescribed genus.

During investigations in the Polish Carpathians we have found specimens of the genus *Pseudachorutella* very similar to two European species, *P. assigillata* (Börner, 1901) and *P. balcanica* Cassagnau et Peja, 1978 described from Germany and Albania, respectively. Examination of the material of the mentioned taxa from Börner's and Cassagnau's collections has enabled us to ascertain that the Polish specimens represent a new species. Its description is presented below.

2. MATERIALS AND METHODS

Litter and rotting wood samples collected in the Polish Carpathians were extracted using a Tullgren apparatus. Obtained specimens of the new species were cleared in potassium hydroxide and chloral phenol and finally mounted on slides in Swan's medium (distilled water, chloral hydrate, glacial acetic acid, glucose, Arabic gum) and observed using a phase contrast microscope Nikon Eclipse E 600. All drawings were prepared using a camera lucida. In order to compare morphology of related species the following material was examined: *P. assigillata*: 4 adult males, 2 adult females, Rotenburg, Germany, 27.03.1927, det. Börner (Börner's collection, housed in Staatliches Museum für Naturkunde Görlitz); *P. balcanica*: subadult male, Greece, det. Cassagnau (Cassagnau's collection, housed in Museum National d`Histoire Naturelle, Paris).

3. TAXONOMY

***Pseudachorutella bescidica* sp. n.** (Figs 1–10, 16–21)

Types. Holotype: adult female on slide, litter and fine debris, deciduous forest, ca. 400 m a.s.l., N slope of the summit Ostra in the "Przełom Jasiołki" reserve near Tylawa village (Beskid Niski Mountains, Carpathians, SE Poland), 16.06.2001, leg. A. Smolis.

Paratypes. Adult male, subadult male, 4 juveniles on slides, same data as holotype. Other material: adult female, in piece of rotting wood, deciduous forest (*Tilio-Carpinetum*), ca. 500 m a.s.l., "Obrożyska" reserve near Muszyna, (Beskid Sądecki Mountains, Carpathians, S Poland), 03.05.2004, leg. A. Smolis, D. Skarżyński. The material is deposited in the collection of the Department of Biodiversity and Evolutionary Taxonomy, Wrocław University, Poland.

Description. Habitus as in Fig. 2. Body length (without antennae) 1.02–2.15 mm (holotype: 1.5 mm). Colour of

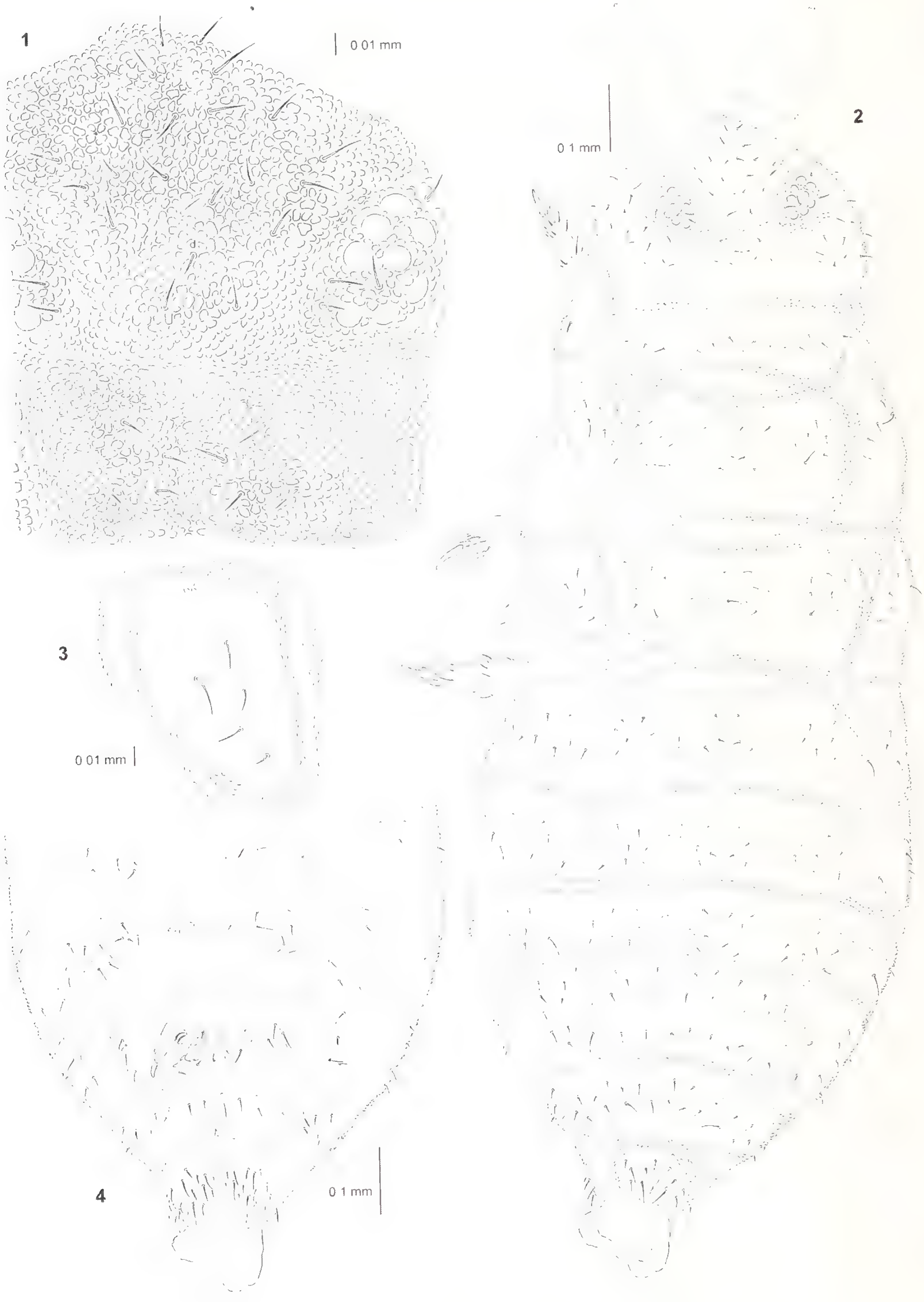


Fig. 1–4. *Pseudachorutella bescidica* sp. n. **1.** dorsal chaetotaxy of central part of head. **2.** habitus and dorsal chaetotaxy. **3.** chaetotaxy of lateral part of tergum III. **4.** chaetotaxy of abdominal sterna II–VI.

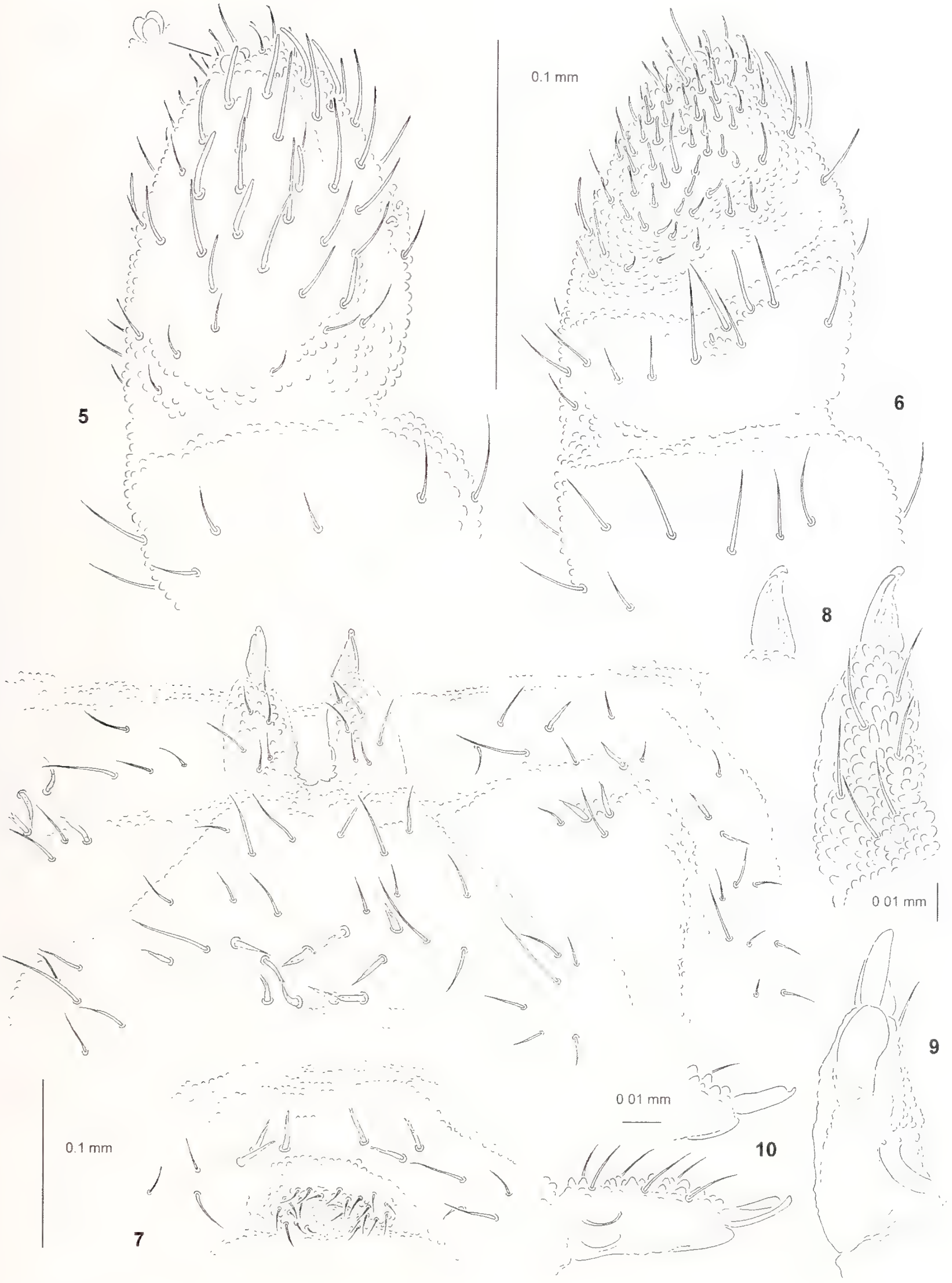
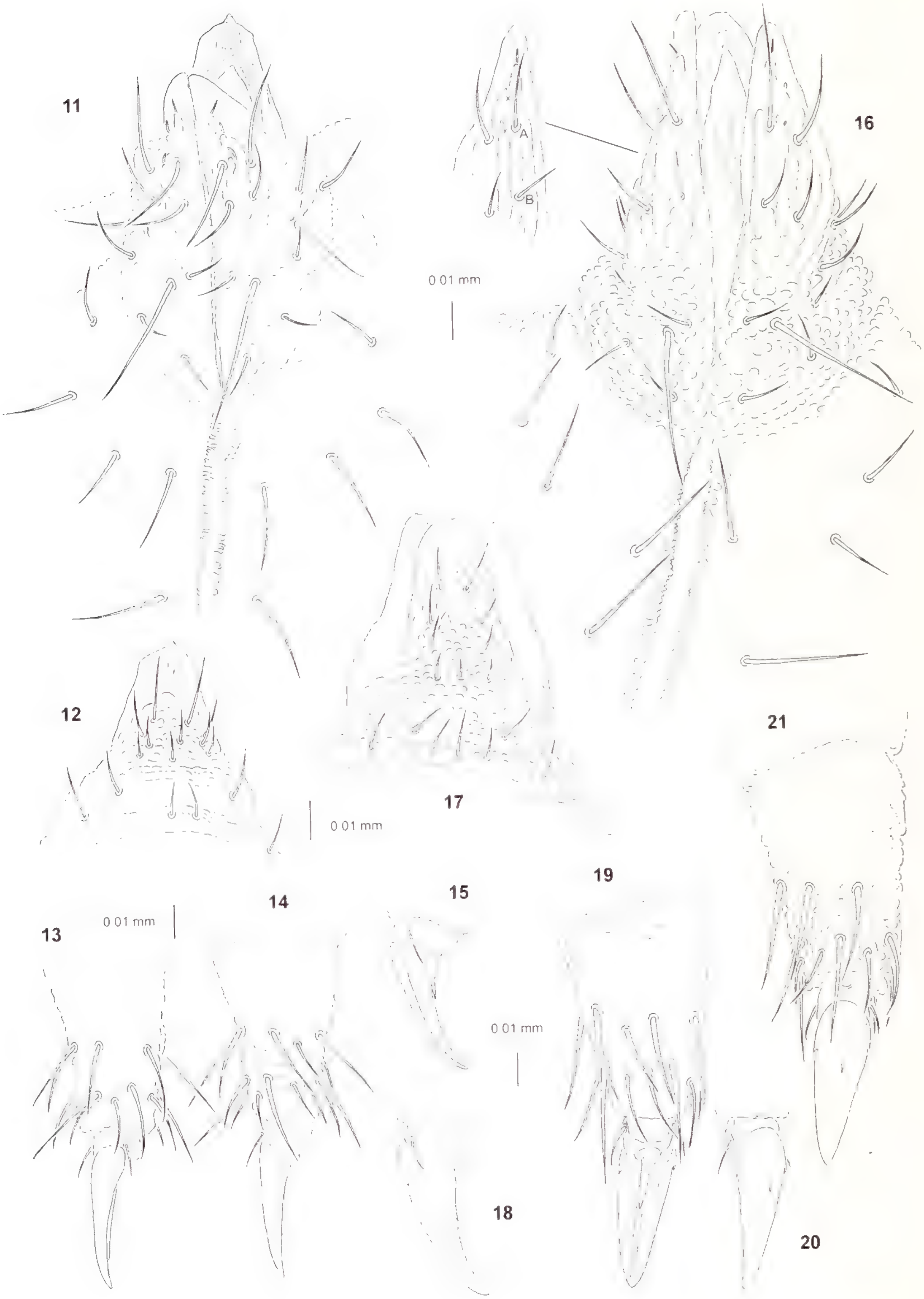


Fig. 5–10. *Pseudachorutella bescidica* sp. n. **5.** antennal segments II–IV of right antenna, dorsal view. **6.** antennal segments II–IV of right antenna, ventral view. **7.** furca, genital plate and male ventral organ. **8.** furca, dorsal view. **9.** furca, ventral view. **10.** furca, lateral view.


11
A
B
16
0.01 mm
12
0.01 mm
17
21
13
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14
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19
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18
20

Fig. 11–21. *Pseudachorutella assigillata* (**11–15**) and *Pseudachorutella bescidica* sp. n. (**16–21**). **11.** labium, **12.** labrum, **13.** tibiotarsus III, dorsolateral view; **14.** tibiotarsus III, ventrolateral view; **15.** claw, lateral view. **16.** labium, **17.** labrum, **18.** claw, lateral view; **19.** tibiotarsus III, ventral view; **20.** claw, dorsolateral view; **21.** tibiotarsus III, dorsal view.

the body grayish-blue, eyes dark. Granulation coarse, rather homogenous (Fig. 1). Antennae shorter than head (Fig. 2). Antennal segment I with 7 chaetae, antennal segment II with 13 chaetae (Figs 5, 6). Antennal segments III and IV fused dorsally. Antennal III-organ with two small internal curved sensilla, one ventral microsensillum and two cylindrical guard sensilla, ventral one slightly longer than dorsal (Figs 5, 6). Chaetotaxy of antennal segments II–IV as in Figs 5, 6. Antennal segment IV with trilobed apical vesicle, subapical organite, microsensillum, chaeta i and 8 relatively thick, cylindrical sensilla (Fig. 5). Antennal segment IV ventrally with numerous modified small sensilla (Fig. 6).

Postantennal organ absent. Area ocularis with 8 + 8 large, pigmented eyes (Figs 1, 2). Buccal cone long. Mandible delicate with 3–4 teeth, maxilla styliform. Labium with 12 + 12 chaetae, 2 + 2 small papillae x and 1 + 1 subapical denticles (Fig. 16). Labium distally distinctly elongated, distance between chaetae A and B greater than length of chaeta B (Fig. 16). Labrum elongated, chaetotaxy: 4–5/2, 3, 2, 2, 2. Labral edge non ogival (Fig. 17).

Dorsal chaetotaxy as in Figs 1, 2. Chaeta d_1 on the head present or absent, unpaired chaeta a_0 absent. Chaetae a_2 on thoracic tergum II and m_1 on abdominal tergum IV present. Dorsal chaetotaxy moderately plurichaetotic, variable. 4–5 ordinary chaetae on lateral parts of terga II–III (Fig. 3). Sensorial formula of the body 022/11111. Sensilla twice as long as ordinary chaetae. Microsensillum on thoracic tergum II present. Thoracic sterna without chaetae, ventral tube with 3–5 + 3–5 chaetae. Ventral chaetotaxy of abdominal sterna II–VI as in Figs 4, 7. Furca relatively long. Dens with 6 chaetae (Figs 7, 8, 10). Mucro 2–2.5 times shorter than dens, triangular in shape (Figs 8, 10). Dens with ventro-apical hyaline area (Figs 9, 10). Retinaculum with 3 + 3 teeth. Male ventral organ (visible only in adult male with ductus ejaculatorius) built of thickened and slightly forked chaetae on abdominal sterna III–V (Fig. 7).

Tibiotarsi I, II, III with 19, 19, 18 chaetae respectively (Figs 19, 21). Femora I, II, III with 13, 12, 11 chaetae respectively. Trochanters with 6 chaetae each. Coxae I, II, III with 3, 7–8, 7–8 chaetae respectively. Subcoxae 2 I, II, III with 1, 2–4, 2–4 chaetae respectively. Subcoxae 1 I, II, III with 1, 2–3, 2–3 chaetae respectively. Claws with one tooth on inner edge, one tooth on outer edge and two lateral teeth (Figs 18–21). Empodial appendage absent.

Derivatio nominis. Named after its terra typica, the Beskidy Mountains in Poland.

Discussion. Among known members of the genus the new species is most similar to *P. assigillata* (Börner, 1901) and *P. balcanica* Cassagnau et Peja, 1978, but differs from them in the following characters: 4–5 ordinary chaetae on lateral parts of terga II–III (moderately plurichaetotic form) (*P. assigillata* and *P. balcanica*: 2 chaetae), distally elongated labium (*P. assigillata* and *P. balcanica*: labium of normal size, see Figs 11, 12), non-ogival edge of labrum (*P. balcanica* also non-ogival, but in *P. assigillata* distinctly ogival, see Figs 11, 12), labral chaetotaxy: 4–5/2, 3, 2, 2, 2 (*P. assigillata* and *P. balcanica*: 4/2, 3, 5, 2, see Fig. 12), male organ present (in *P. assigillata* absent, in *P. balcanica* unknown), four teeth on claws (in *P. balcanica* three teeth, outer tooth absent; in *P. assigillata* only inner tooth present, see Figs 13–15).

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Bonner zoologische Beiträge	Band 55 (2006)	Heft 2	Seiten 81–87	Bonn, Juli 2007

A new species of the genus *Trapelus* Cuvier, 1816 (Squamata: Agamidae) from arid central Africa

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Philipp Wagner & Wolfgang Böhme
Bonn, Germany

Abstract. The Saharo-Sindian genus *Trapelus* contains 14 species, four of which occur in northern Africa. One of these taxa, Trapelus mutabilis, has a very widespread distribution from West to East Africa along the northern Saharan border. It has been identified as a species complex that includes several cryptic taxa. Together with a key of the so far described African species of the genus, the description of the first of these cryptic taxa is presented here.

Keywords. Squamata, Agamidae, *Trapelus* sp. n., Africa, Chad, Ennedi mountains.

1. INTRODUCTION

In his guiding work Moody (1980) revised the family Agamidae and resurrected the genus *Trapelus* Cuvier, 1816. The taxa of the genus are characterized by short and thick heads and a small, deeply sunk tympanum with some spiny scales above the ear-opening. About 14 species of the genus are recognized and are distributed from northwestern Africa, along the Saharan border, through the Near East to southwest and central Asia. Four of them occur in Africa [*Trapelus mutabilis* (Merrem, 1820): northern Africa; *Trapelus pallidus* (Reuss, 1833): Egypt; *Trapelus savignii* (Duméril & Bibron, 1837): Egypt; *Trapelus tournevillei* (Lataste, 1880): Algeria, Tunisia.] with a distribution centre in north-eastern Africa. Most of the Egyptian taxa occur eastwards to the Near East and Egypt is the westernmost border of their distribution. The synonymisation of *T. flavimaculatus* with *T. savignii* by Saleh (1997) is not followed by us in this article, because Saleh (1997) failed to give reasons for this important taxonomic step. The two taxa are clearly distinct both in morphometrics and colouration (Baha el Din 2006), but the former taxon is restricted to Arabia and does not extend into northeastern Africa.

Trapelus mutabilis is perhaps the most complicated and widespread species within the African group. However, it is evident that this taxon represents a species complex including several cryptic taxa. The variability of *T. mutabilis* is already indicated by the high number of synonyms and different descriptions of the species in the relevant literature (Wermuth 1967). For instance, Schleich et al. (1996) referred to blue throated specimens from Cyrenaica (Libya) and mentioned that the taxonomic status of these specimens remained unclear. Further work on a revision of this complex will be done by the authors in the near future.

Trapelus pallidus was also for a time (e. g. Wermuth 1967) considered a junior synonym of *T. mutabilis* but is now again regarded as a valid species (e.g. Pasteur & Bons 1960, Marx 1968, Saleh 1997). Baha el Din (2006) also discussed this topic and drew attention to differences in morphology, colouration, behaviour and habitat. He also mentioned that *T. pallidus* occurs exclusively east of the Nile, whereas *T. mutabilis* occurs west of the Nile.

The new species described herein is closely related to *T. mutabilis* but differs significantly in morphology, body proportions and colour pattern from all other known species of the genus. The *T. mutabilis* complex is distributed in northern Africa [Western Sahara (Geniez et al. 2004), Mauritania (Padial 2006), Morocco (Pasteur & Bons 1960), Algeria (Doumergue 1901), Tunisia (Joger 2003), Libya (Schleich et al. 1996), Egypt (Baha el Din 2006), Mali (Joger & Lambert 1996), Sudan (Geniez et al. 2004)]. Some previously described taxa are currently regarded as synonyms [*Trapelus aegyptius* Cuvier, 1829; *Agama inermis* Reuss, 1833; *Agama gularis* Reuss, 1833; *Agama aspera* Werner, 1893; *Agama latastii* Boulenger, 1885] of this widespread species. Records from the Near East are now known to belong to *Trapelus pallidus* [e. g. Israel, Jordan and Iraq fide Khalaf (1959)].

In addition to the relevant literature we used the material housed in ZFMK (see Appendix) to compare the new species with voucher specimens of the relevant taxa. The synonymy follows Wermuth (1967). Measurements and scale counts were done according to Grandison (1968) and Moody & Böhme (1984). Measurements were taken with a dial calliper to the nearest 0.1 mm.

2. RESULTS & DISCUSSION

Trapelus schmitzi sp. n.

Holotype. ZFMK 2590; Guelta Archei, Ennedi Mountains, Chad; leg. G. Niethammer, April 1954.

Diagnosis. A small species of *Trapelus*, with a short and thick head, a dark throat and a homogenous, smooth to feebly keeled dorsal scalation intermixed with a few larger keeled scales of the same shape. Scalation of hindlimb homogenous. The new species differs from all described African taxa of the genus by its body proportions, a short tail, its dorsal scalation and the uniformly dark-coloured throat.

Trapelus schmitzi sp. n. differs:

- from *T. savignii* (type locality: Egypt) and *T. flavimaculatus* (type locality: Djetta, Arabien) in having smooth ventral scales and in having a very small gular pouch instead a large one.
- from *T. mutabilis* (type locality: Egypt) in having no keeled, enlarged dorsal scales, in a higher number of preanal pores (8 to 12 in *T. mutabilis* [SCHLEICH at al. 1996] instead of two rows of 18 [10+8] in *T. schmitzi* sp. n.), a shorter tail (average of 102.6 mm in *T. mutabilis* and 82.65 mm in *T. schmitzi* sp. n.) and a more or less homogenous dorsal scalation.
- from *T. pallidus* (type locality: 'Oberägypten'= southern Egypt) in having a homogenous hindlimb scalation.

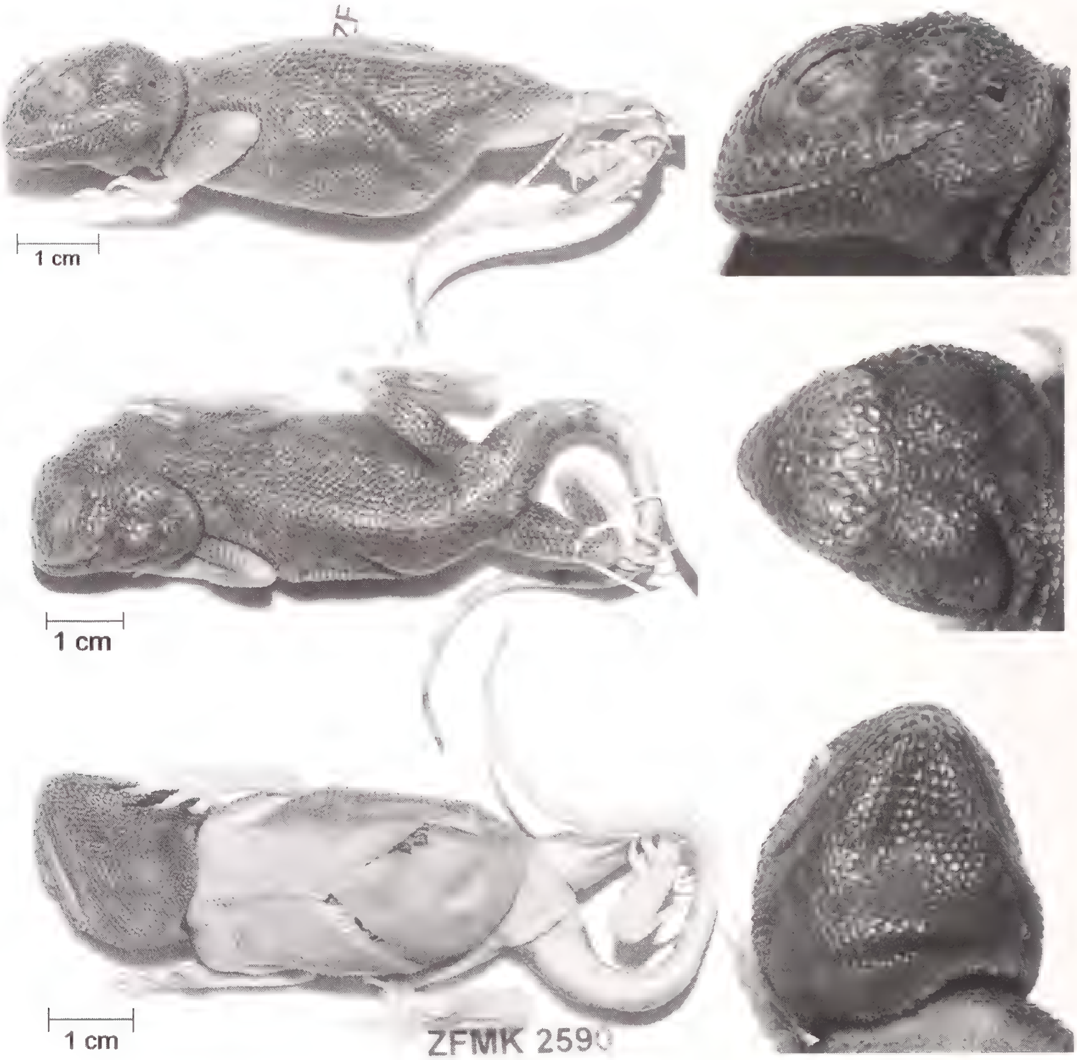

Fig. 1. Holotype of *Trapelus schmitzi* sp. n.

- from *T. tournevillei* (type locality: Ouargla, Algeria) in having shorter body and head proportions, a smaller gular pouch, and smooth to feebly keeled dorsal scales instead of keeled to strongly keeled ventral scales in *T. tournevillei*.

From the available and potentially valid synonyms of *T. mutabilis* (synonymy after WERMUTH 1967) the new species differs as follows:

- from *Agama inermis* Reuss, 1833 (type locality: 'Oberägypten'= southern Egypt) in having smooth to feebly keeled dorsal scales and a more or less homogenous scalation.
- from *Agama gularis* Reuss, 1833 (type locality: 'Oberägypten'= southern Egypt) in having no strongly enlarged dorsal scales and smooth to feebly keeled dorsal scales.
- from *Agama latastii* Boulenger, 1885 (type locality: Egypt) in not having four pairs of quadrangular dark spots, body not depressed and in having a homogenous dorsal scalation intermixed with larger scales.
- from *Agama leucostigma* Reuss, 1833 (type locality: 'Oberägypten'= southern Egypt) in shorter head proportions. The latter has a long head with the broadest point before the ear hole and additionally only two mucronate scales on the superiorly margin of the ear hole.
- from *Agama aspera* Werner, 1893 (type locality: Algerian Sahara between Kef-el-Dhor and Chegga; Biskra-Bordj-Saada; Zab-el-Zig south of El Meranyer) in having smooth or feebly keeled dorsal scales and in having two rows of preanal pores.

Description of the holotype. Habitus stout, tail moderately longer than the body, limbs long.

Measurements. Snout-vent length 69.1 mm; tail length 82.65 mm; head length 20.89 mm; head height 11.7 mm; head width 18.91 mm; length of forelimb 36.84 mm; length of hindlimb 51.5 mm.

Scalation. Nostril on canthus rostralis, pierced in the posterior part of a large, flat nasal scale, directed obliquely upwards. Irregularly arranged smooth scales between nostrils; interorbital region a median row of three more-or-less longitudinal scales separating the sideward originating scales. Supraoculars smooth. Parietal scale more or less round, not enlarged; pineal organ visible, pierced in the middle; parietal scale surrounded by seven slightly enlarged scales. Scales originating from both sides of the parietal midline have their imbrications anteriorly directed, free anterior margins of the scales rarely with sensory pits. Eyelids with a series of mucronate scales forming a ring. Ear-opening small, tympanum sunk, not visible, about one third of the size of eye, its superior margin with four spiny, mucronate scales. Rudimentary nuchal crest of only one spiny, mucronate scale. Gular scales flat, smooth, slightly imbricate at their posterior margins, becoming somewhat smaller towards the gular fold. Gular pouch small. Dorsal scales homogenous, smooth to feebly keeled, partly mucronate, intermixed with few larger and feebly keeled, mucronate scales. Scales on tail smooth, becoming keeled and mucronate posteriorly, not arranged in whorls. Tail cylindrical, 20 % longer than the snout-vent

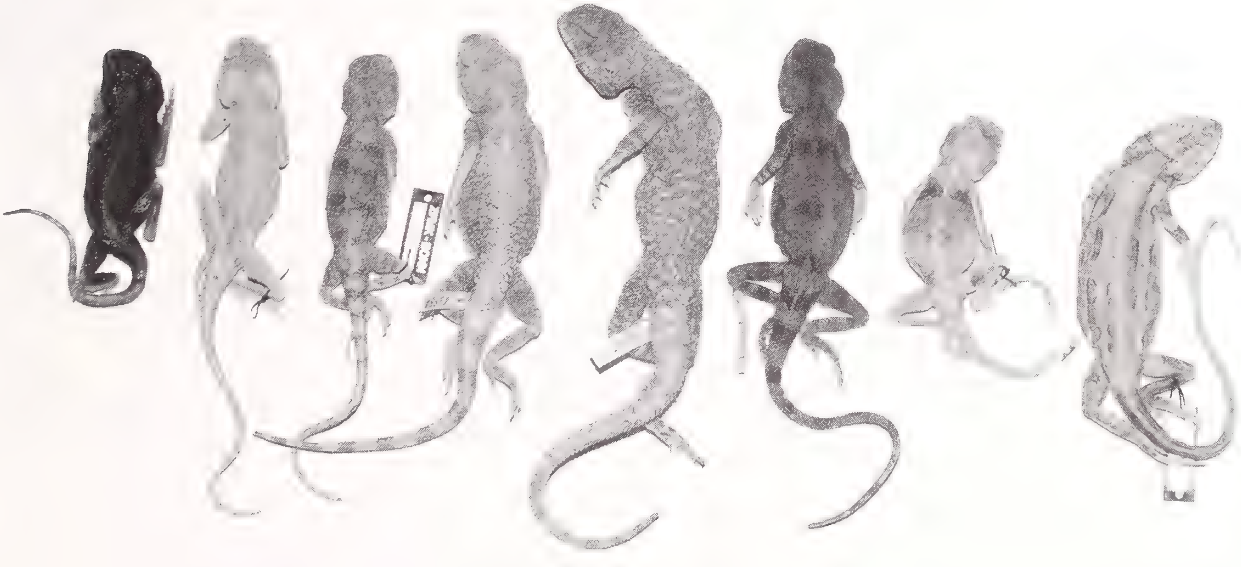

Fig. 2. Holotype of *Trapelus schmitzi* sp. n. in comparison with other African taxa of the genus. From left to right: *T. schmitzi* sp. n., holotype; *T. mutabilis*, Egypt, ZFMK 2520; *T.* aff. *mutabilis*, Sudan, ZFMK 2530; *T.* aff. *mutabilis*, Algeria, ZFMK 49664; *T.* sp. n., Morocco, ZFMK 49751; *T.* sp. n., Morocco, ZFMK 49741; *T. pallidus*, Egypt, ZFMK 2537; *T. tournevillei*, Tunisia, ZFMK 17986.

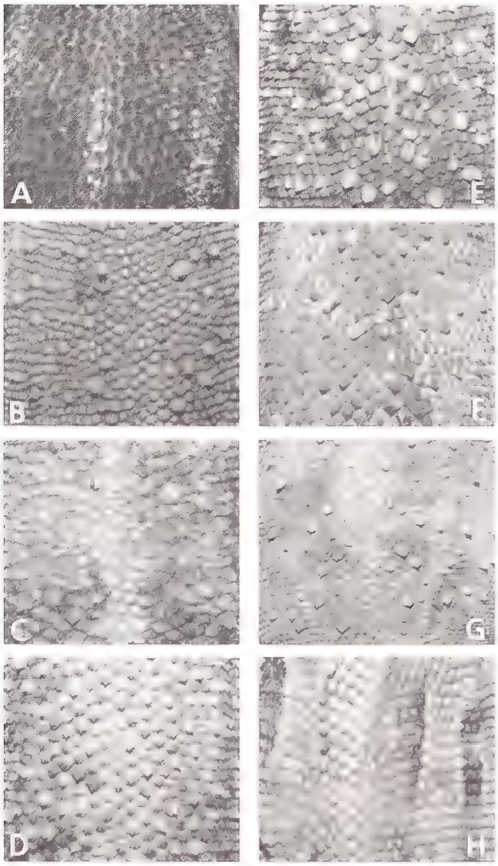

Fig. 3. Dorsal scalation of **A:** *T. schmitzi*, holotype; **B:** *T. mutabilis*, Egypt, ZFMK 2520; **C:** *T.* aff. *mutabilis*, Sudan, ZFMK 2530; **D:** *T.* aff. *mutabilis*, Algeria, ZFMK 49664; **E:** *T.* sp. n., Morocco, ZFMK 49751; **F:** *T.* spec. nov., Morocco, ZFMK 49741; **G:** *T. pallidus*, Egypt, ZFMK 2537; **H:** *T. tournevillei*, Tunisia, ZFMK 17986.

length. Ventral scales smooth and slightly imbricate. Two rows of 18 (10 anterior, 8 posterior) preanal pores. Upper forelimbs with strongly keeled scales becoming feebly keeled beneath, homogenous in size. 4th finger longest, digital length decreasing 3-2-5-1, plantar scales and subdigital lamellae strongly keeled. Scales on hindlimbs homogenous, smooth to feebly keeled and mucronate, becoming more strongly keeled beneath, on the femora as large as the dorsals, becoming slightly larger towards the tibiae and feet. 4th toe longest, digital length decreasing 3-5-2-1, hindlimb long, reaching the eye with the tip of the longest digit.

Colouration in alcohol. Dark grey above without any darker markings, pale vertebral stripe visible, tail annulated dark grey and white, belly and under parts of the tail whitish-grey, gular region uniform dark grey to black, laterally with pale reticulations.

Habitat. If the voucher was collected at Guelta Archei (see below) the habitat is thornbush savannah with sandy soils (see figs. 4 and 5).

Etymology. We dedicate this new species to our good friend and colleague Dr. Andreas Schmitz, Research Officer of Herpetology at the Muséum d´Histoire Naturelle, Genève, Switzerland, in recognition of his valuable contributions to African herpetology.

Distribution and habitat. So far, the new species is only known from the holotype. It was collected by the 'Kollmannsberger International Sahara Expedition' in the Ennedi Mountains in Chad. The specimens collected during this expedition were divided up between several institutions. The specimens collected by Günther Niethammer, a well known German ornithologist, Professor at the University of Bonn and Curator of Ornithology at the Zoologisches Forschungsmuseum A. Koenig, are deposited in Bonn, while specimens collected by Franz Kollmannsberger are deposited in the collection of the University of Saarbrücken. Because the holotype of *T. schmitzi* sp. n. was catalogued shortly after Niethammer's return to Bonn, it belonged to his portion of the material and was thus collected by him. In the Ennedi Mountains, the expedition took two different routes (KOLLMANNSBERGER 1957). Niethammer remained at Guelta Archei to collect birds, while Kollmannsberger crossed the mountains to the northern parts of the Ennedi.

Taxonomic relationships & biogeography. As mentioned in the introduction, *T. mutabilis* is a species complex with several cryptic taxa. *T. schmitzi* sp. n. differs strongly from the typical *T. mutabilis* from Egypt but resembles in some parts of its morphology a population of *T.* aff. *mutabilis* from the Sudan. This hitherto undescribed form (WAGNER unpubl. data) is probably the immediate sister species of *T. schmitzi* sp. n.

This correlates with a biogeographic pattern of the sub-Saharan savanna belt. BÖHME (1985) and MOODY & BÖHME (1984) recognized a distribution gap of typical reptile species of the sub-Saharan belt roughly between Ndélé (Central African Republic) and El Fasher (Sudan). The *Uromastyx acanthinura-geyri-dispar* complex shows nearly the same distribution pattern as the *Trapelus mutabilis* complex. WILMS & BÖHME (2000) differentiated three morphologically distinct clades of which the eastern one, from Tibesti and Ennedi Mountains to Sudan, belongs to *U. dispar dispar*, whereas the western populations belong to *U. dispar maliensis* and *U. dispar flavifasciata*. This distribution pattern suggests that *Trapelus schmitzi* sp. n. might also occur in the Sudan.

Key to the African species of *Trapelus*:

1 – Ventrals keeled; nuptial colouration of males blue, spotted white, tail reddish; females grey with dark crossbars. *T. savignii*

– Ventrals smooth. 2

2 – Hindleg scalation heterogeneous; flat nasal scale, nostril on canthus rostralis, occiput with few spines, no gular pouch, dorsal scales smooth or indistinctly keeled, hindleg scalation heterogeneous, 3rd finger shorter than 4th. *T. pallidus*

– Hindleg scalation homogenous. 3

3 – Dorsal scalation heterogeneous; 3rd finger longer than 4th. Swollen nasal scale, nostril dorsal positioned, occiput without spines, ventrals smooth or feebly keeled, dorsal scales heterogeneous intermixed with larger scales, hindleg scalation homogenous, small gular pouch in males. *T. mutabilis* complex

– Dorsal scalation sub-homogenous; 3rd finger shorter than 4th. 4

4 – Dorsal head scales smooth, four spinose scales on the upper border of the ear-opening dorsal scales equal, smooth to feebly keeled and mucronate, with some intermixed enlarged scales, small gular pouch, dark coloured throat, belly whitish, tail short, little longer as snout-vent-length, two rows of preanal scales in males. *T. schmitzi* sp. n.

– Upper head scales smooth, not enlarged on occiput, no spinose scales on head, very slight fringe of pointed scales on the upper border of the ear-opening, dorsal scales equal, granular, strongly keeled and not mucronate, one row of preanal scales in males, large gular pouch, belly whitish with dark longitudinal stripes, tail long, two and a half as long as the distance from gular fold to vent, covered with equal keeled scales. *T. tournevillei*

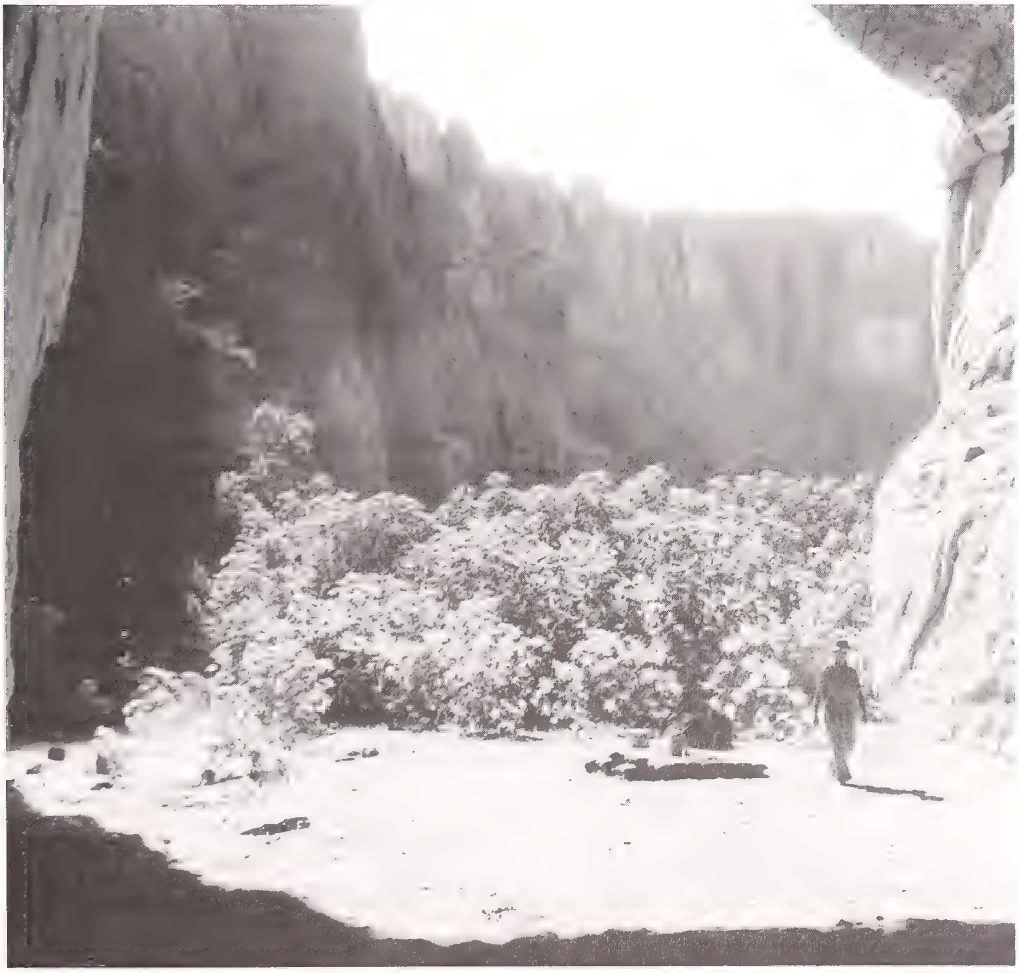

Fig. 4. Habitat of *T. schmitzi* sp. n. around Guelta Archei, Ennedi Mts., at the time of the Kollmannsberger Expedition.

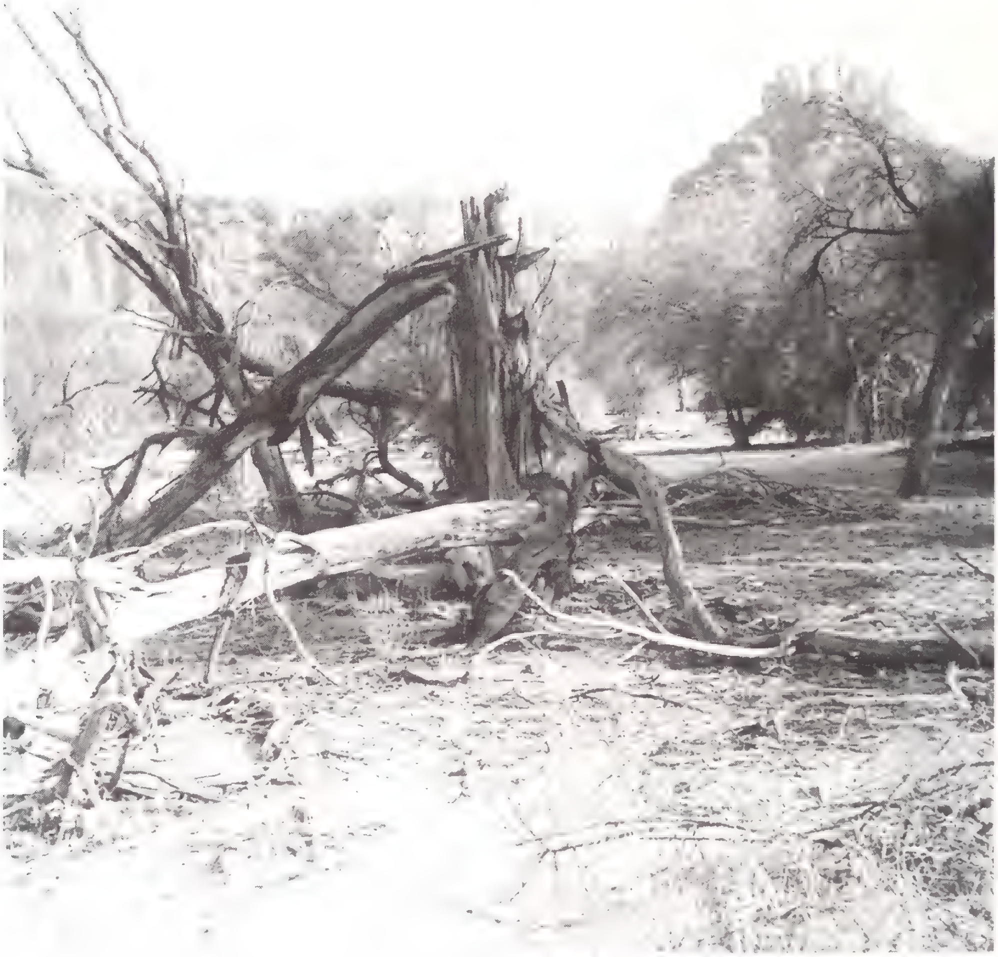

Fig. 5. Habitat of *T. schmitzi* sp. n. at Guelta Archei, Ennedi Mts., at the time of the Kollmannsberger Expedition.

Acknowledgements. We are grateful to Dr. Rainer Hutterer (ZFMK, Bonn) for his supply with the relevant literature and images of the Kollmannsberger expedition and to Dr. Andreas Schmitz (MHNG, Genève) for the review of an earlier draft of the manuscript.

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Appendix

Material examined

Trapelus mutabilis* & *Trapelus* aff. *mutabilis: Algeria: Bechar (ZFMK 49664); Biscra (ZFMK 2487-2490); Bou Sada (ZFMK 49828); Dra el Kastir (ZFMK 2491-2492); El Beioth (ZFMK 2497); Ghardaia (ZFMK 49653-657); Hoggar: Arak (ZFMK 20079), In Eker (ZFMK 20080), Oued Dahim (ZFMK 2498-2499), Thar-emert-Ak (ZFMK 2501-2502), Amguid (ZFMK 2500), Hoggar (ZFMK 2503); Laghout (ZFMK 19416-418); Ouargla (ZFMK 2494-2496); Ounif (ZFMK 7431); Tadmeit (ZFMK 2493); Touggourt: Djamda (ZFMK 2452-2486, 17988). Egypt: Assuan (ZFMK 2517-2518); Kairo (ZFMK 2514-2516, 2519-2526, 2527-2528, 64395-396); Sinai: Abu Muilah (ZFMK 2573), Ain Mouta (ZFMK 2569), Nachla (ZFMK 2565-2568), Sinai (2532-2551), Sudar (ZFMK 64400), Wadi Chbed (ZFMK 2562-2564), Wadi el Arisch (ZFMK 2552-2561), Wadi Feran (ZFMK 77473), Wadi Ramleh (ZFMK 2571-2572), Wadi Schech (ZFMK 2570); Ras Matarma (ZFMK 65474). Libya: Tripolis (ZFMK 20848). Morocco: Akka (ZFMK 49751-754); Erfoud (ZFMK 49741); Ksar EsSouk (ZFMK 7432); Tafilalt: Erfoud (ZFMK 26183). Sudan: Bajuda desert: Chor Abu Harraq (ZFMK 2529-2531); Dafur: Rahib Wells (ZFMK 32471-476). Tunisia: Sousse: Sebkha (ZFMK 2504-2505); Tozeur: Oasis Stil (ZFMK 17987), El Hamma du Djerid (ZFMK 29048-049); Tunisian Sahara (ZFMK 2506-2513). ***Trapelus pallidus***: Egypt: (ZFMK 2537); Jordania: Azrag (ZFMK 44317); Shawbak (ZFMK 44320); Wadi Khanzira (ZFMK 44321). ***Trapelus savignyi***: Egypt: Sinai: Ghaza (ZFMK 2574-2580). ***Trapelus tournevillei***: Algeria: Ain Taiba (ZFMK 2600); Bir Laif: El Alia (ZFMK 2594); El Beioth (ZFMK 2599); El Muilah (ZFMK 2591-2593); El Oued (ZFMK 17984-985); Ghardaia (ZFMK 19415); Ouargla (ZFMK 2597-2598); Touggourt (ZFMK 2595-2596). Tunisia: Hazoua (ZFMK 49571); Oasis Nefta (ZFMK 17986); Tunisian Sahara (ZFMK 2601-2604).

Junker, Thomas (2004): Die zweite Darwinsche Revolution – Geschichte des Synthetischen Darwinismus in Deutschland 1924 bis 1950. Basilisken-Presse, Marburg. 635 S., 25 Abbildungen, mit CD-ROM. ISBN 3-925347-67-4. Preis 124,00 €.

Wo und wann immer die Geschichte der evolutionären Synthese beschrieben wird, geraten nahezu ausschließlich angelsächsische Autoren ins Blickfeld, allenfalls der Russe Sergej S. Chetverikov und – als einziger Deutscher – Bernhard Rensch werden noch als Begründer oder „Architekten" erwähnt (z.B. Mayr 1984, S. 456, Hull 1988, S. 57ff. oder Smocovitis 1996, S. 21). Dass im deutschen Sprachraum sowohl wesentliche Beiträge zur Modernen Synthese entwickelt worden waren, als auch nahezu parallel eine entsprechende umfassende Sicht auf die Evolution der Organismen entstanden war, ist wenig bekannt. Ein erster umfangreicherer Anlauf zur wissenschaftshistorischen Aufarbeitung dieses Abschnitts der Biologiegeschichte war ein Workshop zum Thema „Gab es eine Moderne Synthese in der deutschen Evolutionsbiologie?" am 6. und 7. Dezember 1996 in Tübingen auf Einladung des Lehrstuhls für Ethik in den Biowissenschaften unter Leitung von Eve-Marie Engels. Die Vorträge dieses Workshops wurden 1999 im Verlag für Wissenschaft und Bildung publiziert. (Junker & Engels 1999).

Das vorliegende umfangreiche Werk von Thomas Junker ist ein ungemein detailreiches und gleichzeitig übersichtliches Kompendium aus inhaltlichen Kompaktfassungen wissenschaftlicher Entwicklungen, Biographien beteiligter Wissenschaftler und historischen Analysen von Prozessen und Konsequenzen. Im Abschnitt 1 („Namen – Interpretationen – Rekonstruktionen") werden Begriffe geklärt und werden vor allem die Abläufe in den USA und England denen in Deutschland gegenübergestellt. Der Abschnitt 2 („Die Darwinisten") enthält 29 teils ausführliche Biographien deutschsprachiger Persönlichkeiten aus Genetik, Verhaltensforschung, Morphologie und Systematik, Anthropologie und Wissenschaftstheorie. Unter diesen sind neben den üblichen Prominenten (Konrad Lorenz, Erwin Stresemann, Bernhard Rensch, Gerhard Heberer, Adolf Remane etc.) auch weniger bekannte wie Gertraud Haase-Bessell und Ludwig Rüger. Der Abschnitt 3 behandelt „Die Evolutionsfaktoren" und ventiliert besonders die Formulierung und Gewichtung verschiedener Faktoren in Deutschland. Der vierte Abschnitt („Evolutionstheorie") enthält Würdigungen der deutschsprachigen Beiträge zur Evolutionstheorie allgemein, zur Debatte um Mikro- und Makroevolution, zu Diskursen in der deutschsprachigen Paläontologie und der Beziehungen zwischen der Evolutionstheorie und der Eugenik. Im fünften und letzten Abschnitt („Internationaler Darwinismus") wird – etwas entgegen dem Wortlaut der Überschrift – hauptsächlich die Formierung einer Synthetischen Theorie der Evolution in Deutschland durch die „Architekten" Erwin Baur, Nikolai W. Timoféeff-Ressovsky, Walter Zimmermann und Bernhard Rensch rekonstruiert, und erst auf den letzten zehn Seiten geht es explizit um die internationale Rezeption der deutschsprachigen Synthese.

Abgerundet wird die riesige Daten- und Ideenfülle durch ein Literaturverzeichnis von 83 Seiten – das entspricht knapp 1000 aufgeführten Quellen. Das Buch enthält keinen Index, aber eine CD ROM mit dem kompletten Text des Buches als PDF-Datei. Natürlich erschließt sich der ungeheure Vorteil dieser Kombination nur, wenn man gerade Zugang zu einem Computer mit CD ROM-Laufwerk hat. Das dürfte meistens der Fall sein, denn man wird das vorliegende Buch mit seinen Außenmaßen von 24,8 x 17,5 x 4,5 cm und seinem Gewicht von 1,4 kg wohl eher am Schreibtisch als in der Straßenbahn lesen. Für alle, die bisher innere Widerstände gegen das Medium „Digitales Buch" hegen, sei die gewählte Verbindung von (hervorragend) auf Papier gedrucktem Buch und beigefügter digitaler Version gepriesen. Um wie viel leichter und umfänglicher die Möglichkeiten zur Recherche auf diese Weise als auf herkömmliche sind, kann schwerlich unterschätzt werden.

Der Text liest sich bei aller Komplexität angenehm. Gut gewählte Abbildungen und Tabellen lockern nicht nur das Erscheinungsbild auf, sondern erleichtern es mitunter erheblich, den Überblick über Zusammenhänge zu erwerben oder zu behalten. Die 357 Anmerkungen können zum Glück bei der Lektüre getrost ignoriert werden, sie enthalten in der Tat nur Zusatz-Information. Wäre dem nicht so, hätte es wegen des dauernden Zwangs zum Umblättern von bis zu 500 Seiten eine bedauerliche mechanische Belastung des wunderschön produzierten Buches zur Folge.

Autor und Verleger sind aus Sicht des Rezensenten keine wesentlichen Fehler oder Versäumnisse vorzuhalten. Dass trotz der offenkundig immens ausführlichen Literatur-Recherche und der gründlichen Darstellung des Lebens und des Werks von Wilhelm Ludwig die ungewöhnlich detaillierte und einflussreiche Arbeit von Janis Antonovics nicht zitiert ist, fällt bei der Fülle sonstiger Quellen kaum ins Gewicht. Es kann kaum unbemerkt bleiben, dass im Vergleich zu Genetik und Systematik die Paläontologie deutlich weniger genau beleuchtet wird, und dass zwar „Phylogenie" als Überschrift auftaucht, „Phylogenetik" als Zweig der Evolutionsforschung aber gar nicht behandelt wird. Dies jedoch passt zu einer unverkennbaren Neigung des Autors, Ernst Mayr's Sicht auf die Geschichte der Biologie zu akzeptieren, z.B. in der Kennzeichnung der von Wolf Herre, Adolf Remane und Kurt Kosswig begründeten Phylogenetischen Symposien als „antidarwinistisch". Letztlich liegt es allein in der Kompetenz des Autors, derlei Wertungen vorzunehmen.

Hervorzuheben ist, dass die persönlichen und institutionellen Verstrickungen von Biologie bzw. Biologen und nationalsozialistischer Ideologie und Praxis durchgängig offengelegt und nüchtern dargestellt werden. Dabei ist höchst anerkennenswert, dass der Autor bei aller Offenheit stets jede – möglicherweise ungerechte – moralische Verurteilung der erwähnten Personen vermeidet.

Der doch erhebliche Kaufpreis wird die Verbreitung dieses Werkes bedauerlicherweise deutlich beschränken. Nichtsdestoweniger ist es zur eklektischen Lektüre ebenso uneingeschränkt zu empfehlen wie zum intensiven Studium.

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Populationsgenetische Untersuchungen zur Differenzierung des schleswig-holsteinischen Rehwildes (*Capreolus capreolus* Linnaeus, 1758; Artiodactyla: Cervidae)

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Abstract. Fifty-nine roe deer specimens from four populations in Schleswig-Holstein, northern Germany, were analysed with regard to variability at eight polymorphic microsatellite loci. Two populations were island populations with known reintroduction and translocation histories and two were located on the mainland. The island populations exhibited lower variability as measured by heterozygosity, allelic diversity and allelic richness. Their demographic history is mirrored by the genetic data. Population differentiation was relatively high in terms of occurrence of private alleles (alleles exclusive to only one population) but less so in terms of the overall fixation index, which was only about 6 %, and pairwise genetic distances. Overall deviations from HARDY-WEINBERG expectations were found in all populations studied. Possible explanations include population subdivision (WAHLUND effect) and inbreeding due to small population sizes. The relationship between population viability as seen from the hunters‘ vs. the geneticists‘ viewpoint is briefly discussed in the light of the present study.

Keywords. *Capreolus capreolus*, Schleswig-Holstein, island populations, microsatellites.

1. EINLEITUNG

Das Reh (*Capreolus capreolus* Linnaeus, 1758) ist mit einem geschätzten Bestand von allein in Mitteleuropa etwa 15 Millionen Tieren (MITCHELL-JONES et al. 1999) die häufigste Huftierart des Kontinents. Nach dem beinahe völligen Zusammenbruch des schleswig-holsteinischen Bestandes in der Mitte des 19 Jh. hat das Rehwild mittlerweile ein Rekordhoch erreicht (JESSEN 1988). Entsprechend hoch ist seine Bedeutung auch für die Jagd (Strekke in Schleswig-Holstein im Jagdjahr 2002/2003 über 50.000 Tiere, Jagd und Artenschutz Jahresbericht 2003).

Die vorliegende Arbeit soll einen Eindruck der genetischen Variabilität und Differenzierung, gemessen an acht polymorphen Mikrosatellitenloci, verschiedener Rehwildpopulationen Schleswig-Holsteins vermitteln und überdies die beiden interessanten Inselpopulationen von Föhr und Fehmarn, die sich trotz Isolation und Gründereffekt (s. u.) durch hohe jagdliche Qualität auszeichnen, genetisch charakterisieren.

Der gegenwärtige Rehbestand auf Fehmarn geht auf acht 1935 eingeführte Gründertiere, drei Böcke und fünf Rikken, zurück, nachdem die bereits vor dem Ersten Weltkrieg dort ausgesetzten Rehe wieder ausgestorben waren (NIETHAMMER 1963). Die acht Tiere stammen aus einem Revier von der dänischen Insel Seeland, das sich durch besonders vitales Rehwild (gemessen an Gewicht und Geweih) auszeichnet (ibid.), was die entsprechende Qualität des Fehmaraner Bestandes erklärt, wenn auch bemerkenswert ist, dass sich die Qualität trotz der geringen Größe der Gründerpopulation gehalten hat. Nach Auskunft der ortsansässigen Jäger gelangen keine Rehe vom Festland auf die Insel. Die Analyse dieser Population dient einerseits dazu, die genetischen Folgen der beinahe 70-jährigen Isolation zu charakterisieren, und andererseits kann sie Anhaltspunkte dafür liefern, ob die jagdliche Beurteilung eines Bestandes auf der Basis von Wildgewicht und Trophäenqualität Schlußfolgerungen auf die genetische Variabilität erlaubt oder nicht.

Die Föhrer Population geht auf ein wissenschaftliches Experiment zurück (NIETHAMMER 1963, RIECK 1956): Zur Abschätzung des relativen Einflusses von genetischer Veranlagung und Umweltbedingungen sollte ein neuer Bestand aus besonders starkem Rehwild in einem ungünstigen Habitat und einer aus besonders schwachem Rehwild in einem günstigen Habitat gegründet werden. Derjenige aus starkem Rehwild, für den die Insel Norderney ausgewählt wurde, ging bald zugrunde, so dass der Föhrer Versuch mit schwachem Rehwild blieb. Im Jahr 1939 wurden zwei Böcke und zwei Ricken aus einem Gebiet nordwestlich von Köln sowie ein Bock aus einem Revier westlich von Düren auf der Insel ausgesetzt, jedoch verendeten ein Bock sowie eine Ricke noch in demselben Jahr, so dass die Gründerpopulation aus nur zwei Männchen und einem Weibchen bestand (Rieck 1956). In den Jahren 1958/59 erfolgte eine „Blutauffrischung" mit zehn dänischen Tieren (jeweils fünf Männchen und Weibchen), weil Degenerationserscheinungen vorgelegen hätten (Anonym 1990), die von Rieck (1956) allerdings nicht erwähnt werden. Gleichzeitig bemühte man sich um einen Abschuss des ursprünglichen Bestandes, was aber nicht gelang (ibid.). Zwanzig Jahre später, 1979, wurden abermals fünf dänische Rehe, zwei Böcke und drei Ricken von der Insel Fünen, auf Föhr ausgesetzt, von denen zwei jedoch bald verendeten. Interessant ist, dass die (jagdliche) Qualität der Föhrer Rehe trotz Isolation und Inzucht über dem Landesdurchschnitt liegt und dass bereits in den Fünfziger Jahren, also bevor weiteres Rehwild auf die Insel verbracht wurde, eine deutliche Steigerung von Geweihgröße und Körpergewicht gegenüber den Ursprungsgebieten eingetreten ist (Anonym 1990, Rieck 1956).

Zum Vergleich mit diesen beiden Inselpopulationen wurden zwei durch den Nord-Ostsee-Kanal, der trotz gelegentlicher Überwindung sicherlich ein Migrationshindernis darstellt, getrennte Populationen des schleswig-holsteinischen Festlands herangezogen: eine aus Nordfriesland sowie eine aus dem Kreis Pinneberg (fortan als „Rantzau" bezeichnet).

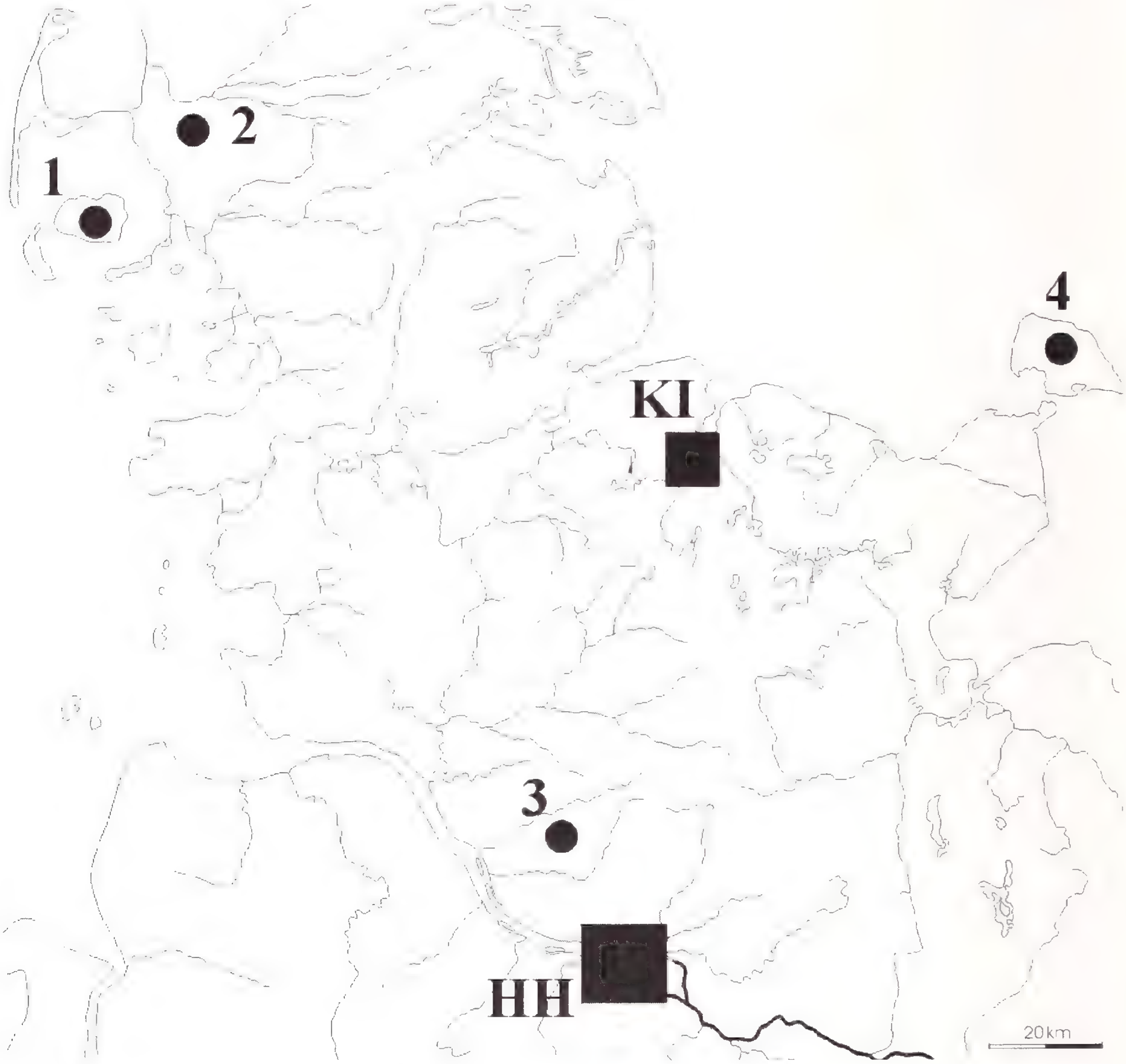

Abb. 1. Geographische Lage der Probengebiete. 1: Föhr, 2: Nordfriesland, 3: Rantzau, 4: Fehmarn. HH = Hamburg, KI = Kiel.

2. MATERIAL UND METHODEN

Es wurden insgesamt 59 Rehe aus vier Populationen untersucht (Abb. 1): Föhr (n = 7), Nordfriesland (n = 10), Rantzau (n = 23) und Fehmarn (n = 19). Die DNA-Isolation erfolgte aus Lebergewebe (entnommen 2003/2004) mit dem SuperQuikGene Kit sowie mit dem DNeasy Tissue Kit. PCR-Amplifikation und -Überprüfung sowie Längenanalyse der Mikrosatelliten erfolgten wie in ZACHOS et al. (2003) beschrieben. Die Annealing-Temperaturen entsprachen den in der Literatur für den jeweiligen Locus angegebenen Werten, wurden bei Problemfällen aber gesenkt. Folgende Mikrosatellitenloci wurden analysiert: OarFCB304 (BUCHANAN & CRAWFORD 1993), RT1, RT7 (WILSON et al. 1997), ILSTS008, ILSTS058 (KEMP et al. 1995), NVHRT16, NVHRT21 und NVHRT24 (RØED & MIDTHJELL 1998).

Mit dem Programm Genepop (RAYMOND & ROUSSET 1995) wurde ein Test auf Kopplungsungleichgewicht („linkage disequilibrium“) durchgeführt, um auszuschließen, dass gekoppelte Loci als scheinbar unabhängige Marker in die Analyse eingingen. Die Alleldiversitäten der Populationen wurden berechnet als die durchschnittliche Anzahl unterschiedlicher Allele pro Mikrosatellitenlocus. Da dieser Index von der Stichprobengröße abhängt, wurde außerdem die sogenannte „allelic richness“ mit der Software Fstat (GOUDET 1995) berechnet. Dieser Wert ist ein Maß für die Allelvielfalt, der um Unterschiede in der Stichprobengröße bereinigt ist, so dass die Werte direkt vergleichbar sind. Beobachtete (H_O) und erwartete (H_E) Heterozygotiewerte sowie ein Test auf signifikante Unterschiede zwischen ihnen (und damit vom HARDY-WEINBERG-Gleichgewicht) wurden mit Arlequin (SCHNEIDER et al. 2000) durchgeführt. Mit Fstat wurde außerdem ein Abweichen vom HARDY-WEINBERG-Gleichgewicht über alle Loci getestet. Als ein Indikator für die Isolation der Populationen voneinander wurden die exklusiven Allele („private alleles“ in der englischen Literatur, SLATKIN 1995), also diejenigen, die in nur einer der untersuchten Populationen auftraten, gezählt. Der Gesamtfixationsindex F_{ST}, der denjenigen Anteil der Gesamtvariation angibt, der auf Unterschiede zwischen den Populationen entfällt (im Gegensatz zu Variation innerhalb der einzelnen Populationen), wurde mit Arlequin berechnet. Um ein weiteres Maß für die Differenzierung der Populationen zu erhalten, wurden mit der Genetix-Software (BELKHIR 2000) paarweise genetische Distanzen berechnet: die Chorddistanz nach CAVALLI-SFORZA und EDWARDS (1967) sowie die für kleine Stichprobengrößen korrigierte Nei-Distanz (NEI 1978).

3. ERGEBNISSE

Alle Loci waren polymorph und wiesen 8 bis 17 Allele auf. Es trat kein Kopplungsungleichgewicht auf (weder mit noch ohne Bonferroni-Korrektur für multiple Tests), so dass alle acht Mikrosatelliten in die Multi-Locus-Analyse einbezogen werden konnten. In den vier untersuchten Populationen fanden sich insgesamt 39 (Föhr), 60 (Nordfriesland und Fehmarn) bzw. 72 (Rantzau) Allele. Die Werte für beobachtete und erwartete Heterozygotie, Alleldiversität, Allelic Richness sowie exklusive Allele sind in Tabelle 1 zusammengefasst. Die Festlandpopulationen weisen – vor allem in bezug auf die Allelic Richness – eine höhere Variabilität auf als die beiden Inselpopulationen, die ein ähnliches Variabilitätsniveau zeigen. In allen vier Populationen traten für einzelne Loci wegen Heterozygotendefizits auch nach Bonferroni-Korrektur signifikante Abweichungen vom HARDY-WEINBERG-Gleichgewicht auf. Auch über alle acht Loci gemeinsam zeigten alle Populationen nach Bonferroni-Korrektur signifikante Abweichungen.

Der Gesamt-F_{ST}-Wert war signifikant von Null verschieden und betrug 0,059. Das bedeutet, dass ca. 6 % der Gesamtvariation auf Unterschiede zwischen den vier Populationen entfallen und ca. 94 % in der Variabilität der Individuen innerhalb der Populationen begründet liegen. Tabelle 2 gibt eine Übersicht über die paarweise errechne-

Tabelle 1. Beobachtete (H_O) und erwartete (H_E) Heterozygotie, Alleldiversität (AD), Allelic Richness (AR), Anzahl exklusiver Allele ("private alleles", P) sowie relativer Anteil der exklusiven Allele für die untersuchten Populationen (FOE = Föhr, NF = Nordfriesland, RAN = Rantzau, FM = Fehmarn). H_O, H_E, AD und AR sind über alle 8 Loci gemittelt.

Pop.	H_O	H_E	AD	AR	P	% P
FOE	0.58	0.80	4.9	4.5	4	10.3
NF	0.64	0.86	7.5	5.5	10	16.7
RAN	0.62	0.82	9.0	5.2	18	25.0
FM	0.55	0.78	7.5	4.6	14	23.3

Tabelle 2. CAVALLI-SFORZA und EDWARDS' Chorddistanzen (oberhalb der Diagonalen) sowie Distanzen nach NEI für kleine Stichprobengrößen (unterhalb der Diagonalen) auf der Basis der Allelfrequenzen von acht polymorphen Mikrosatellitenloci.

	FOE	NF	RAN	FM
FOE	---	0.419	0.386	0.382
NF	0.119	---	0.295	0.156
RAN	0.108	0.098	---	0.254
FM	0.117	0.082	0.081	---

ten genetischen Distanzen zwischen den Populationen. Die Stabilität dieser Werte wird von dem Programm Genetix mit einem Permutationstest geprüft. Dieser ergab sowohl für die Nei- als auch für die Chorddistanz, dass mit Ausnahme der Distanz zwischen Nordfriesland und Fehmarn alle Werte signifikant waren ($p < 0.05$). Beide Distanzmaße zeigen das gleiche Bild: eine geringere Differenzierung zwischen Nordfriesland, Rantzau und Fehmarn als zwischen diesen drei Populationen und Föhr, wobei Nordfriesland jeweils die höchste Distanz zu Föhr aufweist.

4. DISKUSSION

Da die meisten der bisher publizierten populationsgenetischen Arbeiten zum Reh auf Alloenzymen oder Sequenzdaten basieren (z. B. HARTL et al. 1991b, 1993, HEWISON 1995, VERNESI et al. 2002), sind direkte Vergleiche mit der vorliegenden Arbeit nur eingeschränkt möglich sind. Beim Vergleich mit den Ergebnissen von LORENZINI et al. (2002) sowie WANG & SCHREIBER (2001), die Mikrosatellitenanalysen an Rehen aus Italien bzw. Mitteleuropa durchgeführt haben, fällt auf, dass die erwartete Heterozygotie und die Alleldiversität der Rehe aus Schleswig-Holstein höher ausfielen – sowohl für die Festland- als auch für die Inselpopulationen (die Stichprobenunterschiede sind zu gering, als dass sie verantwortlich zu machen wären). Die beiden schleswig-holsteinischen Populationen, die WANG und SCHREIBER im Rahmen ihrer Studie untersucht haben, wiesen erwartete Heterozygotiewerte von 0,50 und 0,54 sowie Alleldiversitäten von jeweils 4,0 auf. Erstaunlich ist, dass für den Locus ILSTS058, den sowohl WANG und SCHREIBER als auch wir analysiert haben, in beiden Studien 16 Allele gefunden wurden, und das obwohl in der vorliegenden Arbeit sowohl der geographische Rahmen als auch die Gesamtzahl untersuchter Tiere (59 gegenüber 492) wesentlich geringer waren. Offensichtlich sind die schleswig-holsteinischen Rehe an diesem Locus besonders variabel.

Die auf ein Heterozygotendefizit zurückzuführenden signifikanten Abweichungen vom HARDY-WEINBERG-Gleichgewicht können mehrere Gründe haben. Neben der Möglichkeit des Auftretens von Nullallelen spielen bei den Inselpopulationen natürlich die geringe Populationsgröße, der Gründereffekt und Inzucht eine Rolle. Schließlich kommt möglicherweise noch die Biologie des Rehs zum Tragen: Die ausgeprägte Territorialität kann dazu führen, dass sich innerhalb eines als panmiktische Population betrachteten Bestandes Untergruppen bilden, was zu einem relativen Anstieg der Inzucht und folglich zu einem Heterozygotendefizit führt (WAHLUND-Effekt).

Die Differenzierung zwischen den Populationen ergibt für beide berechneten genetischen Distanzen ähnliche Ergebnisse. Für die korrigierte NEI-Distanz liegen Vergleichswerte aus der Untersuchung von WANG & SCHREIBER (2001) vor: Die Werte der vorliegenden Studie liegen zwar im Bereich der Werte aus der zitierten Arbeit, sind insgesamt aber – vermutlich wegen des kleineren geographischen Rahmens – durchschnittlich deutlich niedriger. Die Tatsache, dass Föhr die größten Distanzen gegenüber den anderen Populationen aufweist, liegt eventuell darin begründet, dass die Föhrer Population eine Hybridpopulation aus westdeutschen und dänischen Tieren ist. Der F_{ST}-Wert von nur 6 % spricht, im Gegensatz zu der hohen Anzahl an exklusiven Allelen, für eine geringe Differenzierung zwischen den Populationen: LORENZINI et al. (2002, 2003) fanden für italienische bzw. spanische Rehe Werte zwischen 14 und 15%. Ein Test auf Korrelation zwischen genetischen und geographischen Distanzen („isolation by distance") wurde wegen des Inselstatus sowie des allochthonen Charakters der Föhrer und Fehmaraner Rehe nicht durchgeführt.

Unsere Ergebnisse zeigen, dass die Inselpopulationen Föhr und Fehmarn verglichen mit den beiden Festlandpopulationen niedrigere Variabilitätswerte haben. Insbesondere die Fehmaraner Population aber, die auf nur acht Gründertiere zurückgeht, weist eine recht hohe Variabilität im Verhältnis zum erwarteten Grad an Inzucht und Drifteffekten auf. Angesichts dessen könnte man vermuten, dass doch das eine oder andere Reh den Fehmarn-Sund überquert hat oder auf der Insel ausgesetzt wurde, ohne dass schriftliche Vermerke existieren, doch bleibt dies bloße Spekulation. Andere Inselpopulationen zeigen eine deutlich geringere Mikrosatellitenvariabilität, so z. B. die sardischen Rothirsche (ZACHOS et al. 2003 sowie unveröffentlichte Daten) oder, um ein Extrembeispiel zu nennen, die Graufüchse der San-Nicolas-Insel vor Kalifornien, die komplett monomorph sind (cf. AGUILAR et al. 2004)! Die typischen Verinselungseffekte Inzucht und Verlust genetischer Variabilität durch Drift sind auf Föhr sicherlich durch das wiederholte Aussetzen dänischer Rehe aufgefangen worden, doch ist auch hier in der Zukunft mit vermehrter Inzucht zu rechnen. Bemerkenswert ist die Zunahme der (jagdlichen) Qualität des Föhrer Rehwildes bereits relativ kurze Zeit nach der Aussetzung (s. o.), woran zu sehen ist, dass die Realisierung des genetischen Potentials in bezug auf Merkmale wie Körpergewicht und Geweih sensibel auf äußere Einflüsse reagiert. Jagdliche Qualität und genetische Variabilität müssen also nicht zwingend miteinander korreliert sein. Das darf indes nicht darüber hinwegtäuschen, dass Inzucht und genetische Verarmung in kleinen, isolierten Beständen unweigerlich zunehmen. Dazu kommt, dass an Geweihmerkmalen ausgerichtete selektive Bejagung mit diesen Merkmalen gekoppelte Loci ebenfalls einem gerichteten Selektionsdruck aussetzt (cf. Hartl et al. 1991a, 1995a, b sowie Scribner & Smith 1990), der nicht unbedingt den Selektionsbedingungen im Naturzustand entspricht. Eine gute jagdliche Qualität des Wildes sollte auf keinen Fall mit fehlender Inzuchtgefährdung gleichgesetzt werden, deren Folgen oft erst relativ spät im Zusammenspiel mit genetischer Verarmung phänotypisch sichtbar werden, und auch dann nicht notwendigerweise an den Merkmalen, die der jagdlichen Beurteilung zugrunde liegen.

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Bioacoustic Characteristics and Population Numbers of Endemic *Cinclodes oustaleti baeckstroemii* (Aves: Furnariidae) Lönnberg, 1921 of Alejandro Selkirk Island, Chile

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Abstract. Two types of vocalisation of the endemic Masafuera Grey-flanked Cinclodes *Cinclodes oustaleti baeckstroemii* Lönnberg, 1921 are distinguished: contact call and song. The call is a whistle-like "chic" similar to that of the mainland taxon *C. o. oustaleti.* The song is described for the first time and illustrated by sonagrams. It is a low, melodic series of pearling notes uttered early in the morning. Song sequences vary in duration, being about two to five seconds long. The frequency amplitude of elements ranges from 5.3 to 7.7 kHz, showing core frequencies from 5.8 to 6.8 kHz. Elements are usually separated by pauses of about 0.03 seconds. At the beginning and end of a sequence the song pauses are extended up to 0.15 seconds. The song is low and only heard for a short distance, maybe as it is addressed to the partner at one specific site. The first census counts of this endemic species were carried out using the line transect method. Both estimates of its population size (in the years 1994/95 and 2002) resulted in a total number of approximately 1500 individuals. Thus no negative population trend was detected; however, this small population confirms the "vulnerable" conservation status of the Masafuera Cinclodes. Conservation management should include further population monitoring and eradication of introduced mammals.

Keywords. Vocalisations, song, call, Masafuera Grey-flanked Cinclodes, Juan Fernandez, *Cinclodes oustaleti baeckstroemii*, transect method, island census, conservation basis.

Resumen. Dos tipos de vocalización del endémico Churrete chico de Másafuera *Cinclodes oustaleti baeckstroemii* Lönnberg, 1921 fueron distinguido, grito de contacto y canto. El grito es un gorjeo ("chic") similar a eso del *C. o. oustaleti* en tierra firme. El canto ha sido descrito para primera vez y esta ilustrado por sonagrames. El canto es una serie de tonos bajos y melódicos cantado temprano en la mañana. Secuencias de canto pueden variar en su duración, por lo menos de dos a cinco segundos. La frecuencia de los elementos tiene un rango de 5,3 a 7,7 kHz con una frecuencia principal de 5,8 a 6,8 kHz. Elementos usualmente están separados por pausas de próximamente 0,03 segundos. En el inicio y fin del canto pausas están alongadas hasta 0,15 segundos. La rara y baja presentación del canto da indicación para la ausencia de una adaptación vocal compensativa a las condiciones isleñas ventosas. Usando el método de transectos lineares, dos censos de la población han sido realizados (en los años 1994/95 y 2002), que han sido resultados en un numero total de próximamente 1500 individuos en Isla Alejandro Selkirk. Por eso no tendencia critica de la población ha sido detectada, pero el Churrete chico de Másafuera es clasificado como vulnerable. Manejo de conservación debe incluir monitorio de su población e erradicación de mamíferos introducidos.

Zusammenfassung. Zwei Typen der Lautäußerung des endemischen Masafuera-Grauflanken-Uferwippers (*Cinclodes oustaleti baeckstroemii* Lönnberg, 1921) werden unterschieden: Kontaktruf und Gesang. Der Ruf ist ein pfiffartiges „tschick" ähnlich dem von *C. o. oustaleti* auf dem Festland. Der Gesang wird hier erstmals beschrieben und durch Sonagramme illustriert. Er ist eine leise und melodisch vorgetragene Serie perlender Töne, die am frühen Morgen geäußert wird. Gesangssequenzen können in der Länge von etwa zwei bis fünf Sekunden variieren. Die Frequenzamplitude von Elementen reicht von 5,3 bis 7,7 kHz bei einem Kernfrequenzbereich von 5,8 bis 6,8 kHz. Elemente werden durch kurze Gesangspausen von ca. 0,03 Sekunden voneinander getrennt. Am Anfang und Ende der Gesangsstrophe sind die Pausen bis zu 0,15 Sekunden verlängert. Der leise und nur in geringer Distanz vernehmbare Gesang ist möglicherweise an den Partner an einem bestimmten Ort adressiert. Mittels der Linien-Transekt-Methode wurden die ersten Populationserfassungen dieses Endemiten durchgeführt. Die darauf basierenden Gesamtbestandszahlen führten in den Jahren 1994/95 sowie 2002 jeweils zu einer Anzahl von etwa 1500 Individuen auf Alejandro Selkirk. Demnach wurde zwar kein negativer Populationstrend festgestellt, aufgrund der kleinen Populationsgröße ist jedoch der Gefährdungsstatus („vulnerable") für den Másafuera-Uferwipper zutreffend. Schutzmaßnahmen sollten ein weiteres Bestands-Monitoring und die Bekämpfung eingeschleppter Säugetiere beinhalten.

1. INTRODUCTION

The Juan Fernandez Islands are the most important endemic bird area of Chile and host more endemic bird taxa than any other region of this country (cf. Wege & Long 1995). However, they face severe conservation problems as for example seen by the low population size of another endemic landbird species, the Masafuera Rayadito *Aphrastura masafuerae* (Philippi & Landbeck, 1866) (Philippi & Landbeck 1866; Brooke 1987; Hahn 1998). For the endemic Grey-flanked Cinclodes *Cinclodes oustaleti baeckstroemii* Lönnberg, 1921, a population census had never been carried out. Together with *Aphrastura masafuerae* it represents a biogeographical outpost of the Neotropical ovenbird family (Aves: Furnariidae), being limited to only Juan Fernandez in the South-east Pacific (cf. Schlatter 1987).

The collector Bäckström (Lönnberg 1921) and later observers (cf. Johnson 1967) reported *Cinclodes oustaleti baeckstroemii* from Alejandro Selkirk as well as from Robinson Crusoe islands. Interpreting these sources, the population on Robinson Crusoe appears to have been smaller and more oscillating than that of Alejandro Selkirk. However, probably due to lack of adequate data, recent reviews do not differ between islands, and simply state the entire Juan Fernandez Archipelago as the distribution area, therefore including also Santa Clara (Jaramillo 2003; Remsen 2003). Due to its insular distribution area and the general conservation problems of the archipelago, this endemic cinclodes was already classified as "vulnerable" in the red list of terrestrial vertebrates of Chile by Glade (1993).

Little is known about its population and biology in general, partly in relation to the remoteness of the islands and the badly accessible terrain. An additional difficulty hampering any population census was the fact that its vocalisations had not been described. However, reliable census data are fundamental for any conservation management. Presenting the first description of vocalisations and the first population data, I aim to provide basic information for the endemic Másafuera Cinclodes. It may help researchers and managers to acoustically identify individuals in the field, and to monitor the population in the future.

2. METHODS

The study area is Isla Alejandro Selkirk (formerly Másafuera), the westernmost island of the Juan Fernández Archipelago (33°45'S and 80°45'W). Alejandro Selkirk is in the South-east Pacific 167 km west of the other major island Robinson Crusoe, and 769 km off the coast of Chile. The archipelago is biogeographically isolated by lacking any neighbouring islands within a 500 km-zone, and the cool Humboldt Current separating it from the South American continent. Alejandro Selkirk (44.64 km?) is of young volcanic origin, shaped like a big rock dome and is one of the steepest islands worldwide. It is entirely part of the Juan Fernández national park founded in 1935, and UNESCO Biosphere Reserve since 1977. More detailed geographical descriptions may be taken from Castilla (1987) and Skottsberg (1920–1956).

Field work was carried out on the island during the austral summers from 25 November 1992 to 1 February 1993, 15 December 1994 to 9 February 1995, and 23 January to 8 February 2002. Visual field identification of birds was straight foreword, basing on Araya et al. (1992; cf. also Jaramillo 2003) and the original description (Lönnberg 1921). Acoustic identification was possible after learning the bird vocalisations while they were under visual observation and taping with a DAT-Recorder (Sony, Type HD–S100). An ordinary external microphone with additional wind protection was placed in suitable field position. Evaluation of the tape recordings was done with the program AVISOFT-SONAGRAPH PRO.

For the estimation of bird populations a number of methods have been developed during the past decades (overviews in Ralph & Scott 1981; Bibby et al. 2000). The abundance data should reach a high level of comparability and cover a maximum area. Therefore the line transect method was chosen (description by Emlen 1971, 1977). Although a quantitative method is determined to be efficient if two-thirds of the present birds are recorded (Eberhardt 1978), I aimed to record a significantly higher portion. Thus, I chose a small transect width, and tried to record birds by visual as well as vocal contact. On the Juan Fernandez Islands a total of 111 line transect counts were carried out from 1992 to 2002. Different transect areas and habitat types were covered (for details see Hahn 1998).

3. RESULTS

Cinclodes oustaleti baeckstroemii is a small brownish-grey bird of generally inconspicuous appearance, showing long white-framed tail feathers, a whitish superciliar stripe, and a small body size (cf. also Fjeldså & Krabbe 1990; Ridgely & Tudor 1994; Remsen 2003). It flicks its tail up and down like a wagtail, often in the vicinity of water in a brook. It searches rocks, boulders, stone walls, mosses, and lichens for arthropod prey, flying mostly for short duration and distance only. Even in flight the bird reminds to wagtails (*Motacilla*), for example when dynamically manoeuvring with its long tail to follow a flying insect.

It mostly lands on top of stones, rocks or other open places. Only rarely it may land on ferns or other tall plants. No individuals were observed inside the vegetation.

Description of vocalisation types

Two principal types of vocalisation were identified: call and song. The call is a monotonous "chic" or may also be titled a whistle-like call. It is uttered very similar throughout the whole genus, either single or in a loose series of calls. The song of this endemic taxon was recorded for the first time and is described here through sonagrams (Figs. 1 & 2). It is uttered in the early morning by only one individual of the pair (probably the male). The song is a melodic series of pearling notes.

Song elements are limited to frequencies between 5.3 and 7.7 kHz (Fig. 1a). Within this amplitude the extension of elements varies and a wave-like structure is recognised. In Figure 1b it is visible that the frequency of song elements is slightly different. Single elements are mostly open below or sometimes have the structure of an "S" laid on its side (e.g., last element of Fig. 1b). The short sequence (Fig. 2) illustrates the most covered frequency level of 5.8 to 6.8 kHz. This corresponds to frequency amplitudes of single elements covering about one kilo hertz (kHz). At the beginning and end of the sequence single elements are arranged looser/slower (0.1–0.15 sec.), whereas in the central song elements are closer to each other, and thus following faster with pauses of approximately 0.03 seconds.

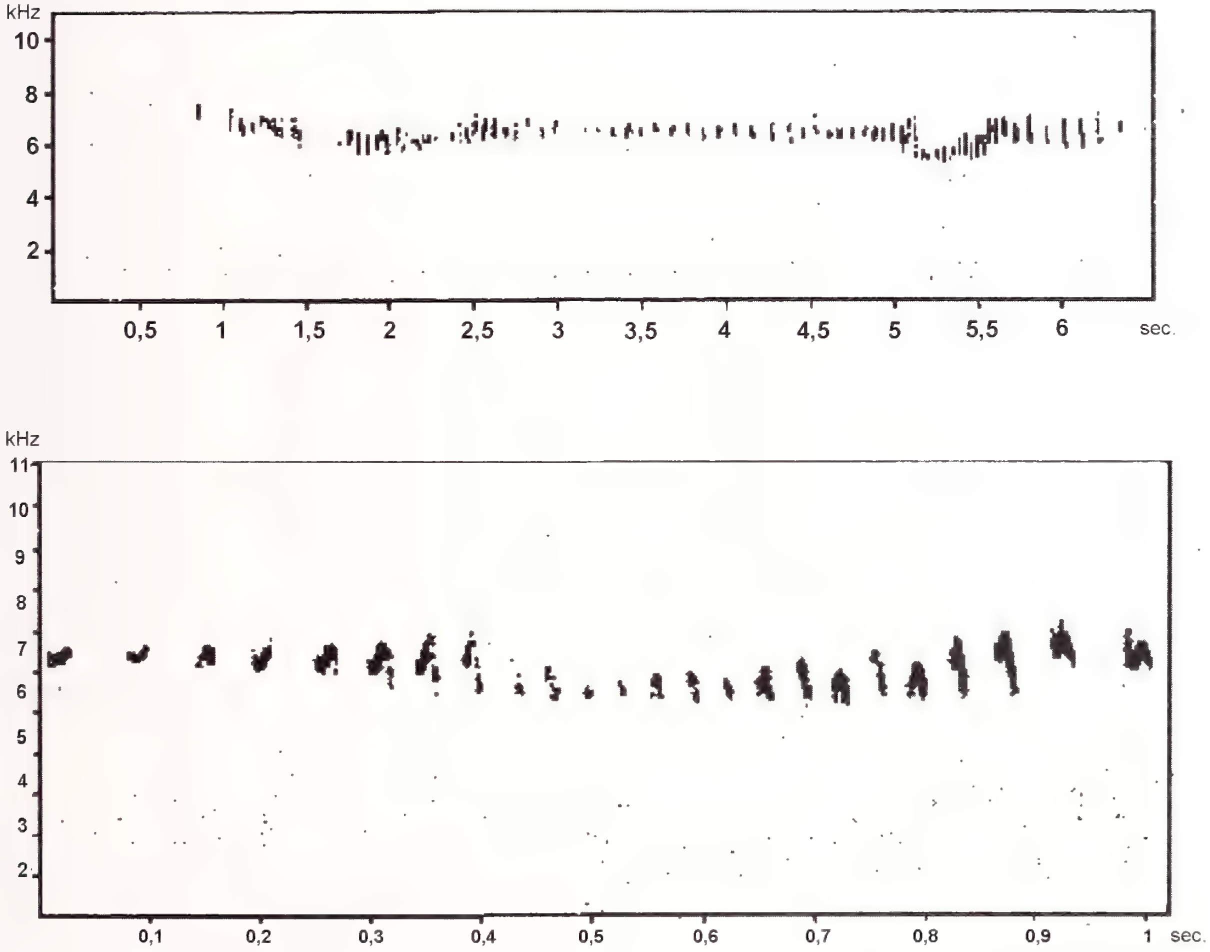

Fig. 1 (a & b). Song of the Másafuera Grey-flanked Cinclodes *Cinclodes oustaleti baeckstroemii* Lönnberg, 1921 on Alejandro Selkirk Island. A) Long sequence of 5.5 seconds (N=256, F=100, O=0, kHz =22); B) Section of A of 1 seconds duration (from 4.75 to 5.75 sec. on the time scale) (N=512, F=50, O=93.5, kHz =22.05); Evaluation levels of the program AVISOFT-SONAGRAPH PRO are given in parentheses.

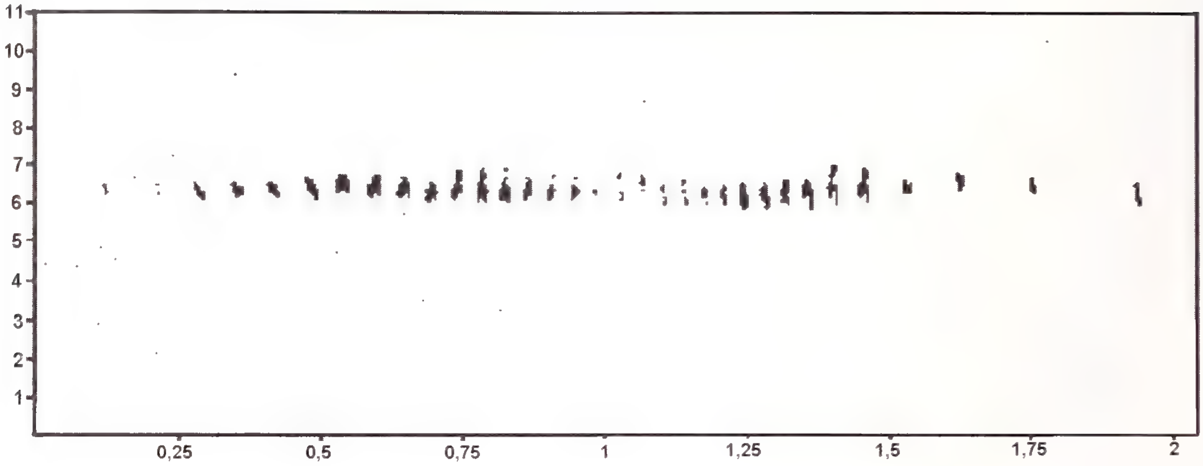

Fig. 2. Song of the Másafuera Grey-flanked Cinclodes *Cinclodes oustaleti baeckstroemii* Lönnberg, 1921 on Alejandro Selkirk Island. Short sequence of 1.8 seconds duration (N=512, F=50, O=88, kHz =22).

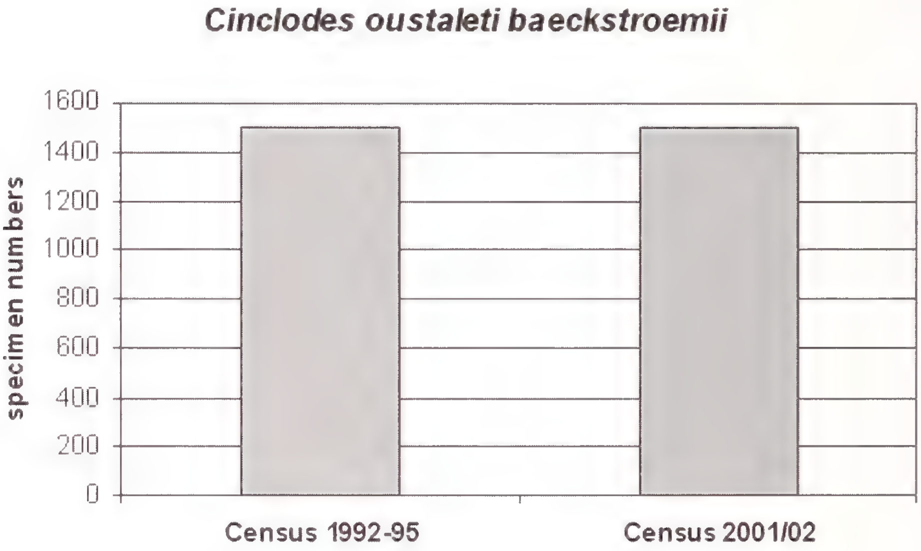

Fig. 3. Total population numbers of the Másafuera Grey-flanked Cinclodes *Cinclodes oustaleti baeckstroemii* Lönnberg, 1921 on Alejandro Selkirk Island in comparison of two census periods. Censuses were carried out using a modified version of the line transect method (cf. HAHN 1998).

Population numbers

During census counts and additional observations from 1992 to 2002 no Masafuera Cinclodes specimen was observed on the islands Robinson Crusoe and Santa Clara. This is an important result, as *C. o. baeckstroemii* was repeatedly observed on Robinson Crusoe during the last century (LÖNNBERG 1921; JOHNSON 1967), and even recent reviews state the whole Juan Fernandez Archipelago as the distribution area (JARAMILLO 2003; REMSEN 2003). On Alejandro Selkirk they were recorded during eight transect counts with 49 specimens, and mapped during numerous non-transect excursions. Thus the Masafuera Cinclodes is presently interpreted to be endemic only to Alejandro Selkirk, in spite of the fact that single individuals also have been seen on Robinson Crusoe in the past (LÖNNBERG 1921). They inhabit all elevation levels up to the top of the summit of Los Inocentes (1320 m) and may be found in all habitat types. Preferred landscape structures are the washes and V-shaped Quebradas, which also carry water in the summer; for example, the Quebradas Tongo, Varadero, Inocentes, Vacas, Casas, Sanchez, and Guaton. The rocky beaches are only occupied where freshwater is nearby, for example at the end of Quebrada Inocentes. However, Másafuera Cinclodes may be abundant in some upland regions too, where no permanent waters exist, namely in moist areas often covered with clouds. Few specimens were seen resting on the top of tall plants or visiting dry grasslands where no washes are nearby.

Only a very few indicators exist to reconstruct the population development of *Cinclodes oustaleti baeckstroemii*. In the year 1917, Bäckström (LÖNNBERG 1921) called them "common" in certain regions of Alejandro Selkirk. In the year 1986, BROOKE (1987) made a similar general statement. In 1994/95 I carried out the first census of this cinclodes, which resulted in an estimate of about 1500 individuals. On this set of data no population trend or any type of fluctuation can be reconstructed for historical times. It seems that this endemic taxon was widely distributed and quite common on Alejandro Selkirk during the last century. The 2002 census also led to a size of approximately 1500 specimens. Thus no changes in the population size have taken place within this seven year period. Also no significant differences were found by comparing exactly the same three transect routes on Alejandro Selkirk in 1994/95 (20 individuals) and in 2002 (19 individuals).

4. DISCUSSION

The common call of *C. o. baeckstroemii* sounds very similar to that of *C. o. oustaleti*, and even to some other species of *Cinclodes* on the mainland. Its primer function seems to keep vocal contact between two partners or members of a family party. The song of *C. o. baeckstroemii* is a fine and rather low vocalisation type that is not heard beyond a distance of more than 100 m. Thus, no obvious audible adaptation to the harsh and windy conditions on this oceanic island can be identified. In contrast, two other endemic landbirds (*Aphrastura masafuerae* and *Sephanoides fernandensis*) have developed significantly louder and/or more intense vocalisations on the Juan Fernandez Islands (e.g., HAHN & MATTES 2000).

Another remarkable fact is that only a very few singing *C. o. baeckstroemii* were observed, and few songs were heard throughout the entire study time. This is remarkable as cinclodes were not rare on the island, present in many habitat types, and holding territories in most regions. Maybe singing is more frequent in early spring and largely decreased when males are bound in pairs. This represents a difference to the island's other endemic furnariid (*Aphrastura masafuerae*), which continues to sing every morning even during breeding and nestling time. Sonagram comparisons with mainland *C. o. oustaleti* are not yet possible, as tape-recordings of this form are lacking. The total population size of about 1500 corresponds to an average density of 3.4 individuals per 10 hectares. This seems to represent a realistic value, taking into account that the well-watered canyon bottoms are the preferred habitat, and that pastures or other dry areas remain uninhabited. Through the impact of fires and introduced goats the open habitats increased on the island since discovery in 1574. Through such destruction of vegetation, several of the canyons in the North of the island carry no water during summer, but probably have done so when the vegetation was intact. Thus, many northern canyons presently are not inhabited by *C. o. baeckstroemii* due to lack of freshwater.

Another threat comes from introduced predators. Cats *Felis catus* f. catus (Linnaeus, 1758), Norway rats *Rattus norvegicus* (Berkenhout, 1769), Ship rats *R. rattus* (Linnaeus, 1758), and House mice *Mus musculus* (Linnaeus, 1758) have landed on Alejandro Selkirk, and have grown wild (HAHN & RÖMER 2002). At least cats and mature rats are able to prey on adult passerine birds (RÖMER 1995), but all four are known to prey on bird broods. The impacts of these pest species on the population of the Másafuera Cinclodes have not yet been investigated. Taking into account its small distribution range, especially the absence from Robinson Crusoe, this endemic species should be upgraded in the Chilean Red List from "vulnerable" (GLADE 1993) to "endangered". The population size shows no critical trend, but should be monitored for a five-year interval. The principal conservation goal must be the eradication of all introduced mammals, but for efficiency reasons campaigns should start with goats.

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Biogeographical Isolation and Bioacoustics: the Juan Fernandez Firecrown, *Sephanoides fernandensis* (Aves: Trochilidae) (King, 1831), of Robinson Crusoe Island, Chile

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Abstract. Three types of vocalisation of the endemic Juan Fernandez Firecrown, *Sephanoides fernandensis* (King, 1831), are described: courtship song, warning whistle, and territorial call. The first sonagrams of this hummingbird species are presented. Territorial vocalisations are most commonly uttered and are important to localise individuals on Robinson Crusoe Island, Chile. Although in the bioacoustic analysis significant differences between the three vocalisations are identified, they have one general character in common: audibility over a relative long distance. In this point these vocalisations also differ from those of its closest continental ally, the Green-backed Firecrown *S. sephaniodes*, and may represent an adaptation to the harsh island conditions and oceanic winds.

Keywords. Vocalisation, song, call, *Sephanoides fernandensis*, island adaptation.

1. INTRODUCTION

The endemic Juan Fernández Firecrown, *Sephanoides fernandensis* (King, 1831), is biogeographically the most isolated species of all hummingbirds (Aves: Trochilidae), being limited to only one small island in the South-east Pacific Ocean (Isla Robinson Crusoe: 47.11 km^2, 915 m high, 567 km distant to the mainland at 33°30'S & 78°50'W). The species has been separated from its mainland ancestors for some 600,000 years (Roy et al. 1998). Males and females show the most significant sexual dimorphism and dichromatism of all investigated Trochilidae (Colwell 1989), and also seem to differ from each other in various ecological aspects. However, little is known about the ecology of this island endemic in detail, except that it is in threat of extinction and therefore classified as "critically endangered" (Roy et al. 1999; BirdLife International 2004). This partly may be due to anthropogenic habitat destruction, competition, and predation by introduced mammals (Busse 1970; Hahn & Römer 2002). Its vocalisations are still undescribed (cf. Jaramillo 2003). However, a successful conservation management requires basic information on aut-ecology. Attempts to reliably estimate the population size (Brooke 1987; Meza 1989; Stiles 1987; Stone et al. 1989; Hahn 1998) require the knowledge of its vocalisations. This is especially important as its closest mainland relative, the Green-backed Firecrown *Sephanoides sephaniodes* (Lesson & Garnot, 1827), reached Robinson Crusoe between 1574 and 1830 (cf. Audouin 1830) and now competes with it for food sources. Presenting the first data of the Juan Fernández Firecrown's bioacoustics, I aim to add more scientific information of this endemic and to provide basic material that may help future researchers and managers to acoustically identify individuals in the field.

On the basis of four field campaigns from 1992 to 2002, three main types of vocalisation have been identified: courtship song, warning whistle, and territorial song/call. The courtship song is a purring series of syllables, uttered without pause at comparatively low-pitched frequency levels (around 4–5 kHz) and high temporal rates, slightly falling and rising in pitch. It was recognised from the male, which was slowly flying behind the female and following her from a distance of about 50 cm. The warning call is a short and very high-pitched (8 kHz and more) whistle, which is uttered by both sexes. It may be heard during intra- and inter-specific conflicts with other (humming)birds or in case of the presence of potential predators (e.g., cats, rats, humans). This whistle is difficult to distinguish from Green-backed Firecrown vocalisations in the first instance. Most characteristic and most commonly uttered are territorial song and calls. Male Juan Fernandez Firecrowns are much more abundant than females on the island and, regarding to their larger size and physical dominance, are much more territorial. Thus, most such songs / calls which a listener may hear in the field come from males (Fig. 1), but females utter them too.

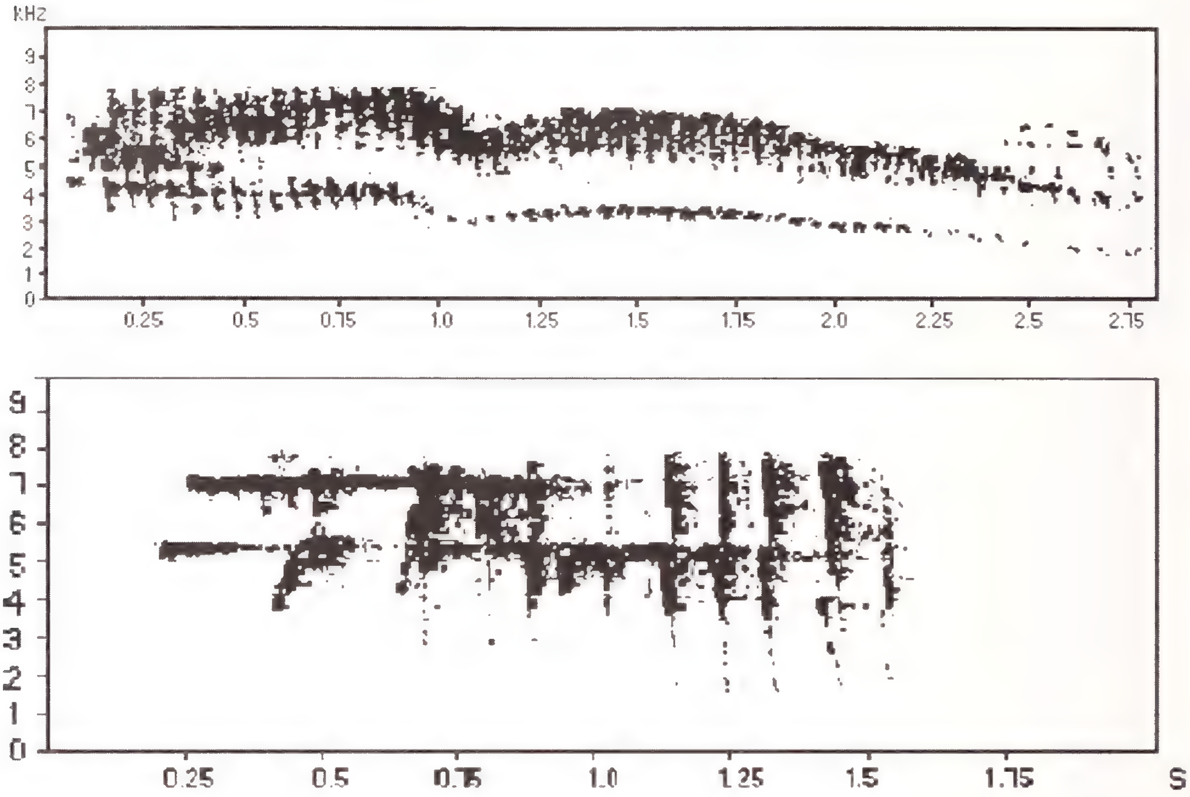

Fig. 1. Territorial vocalisations of the Juan Fernandez Firecrown *Sephanoides fernandensis* (KING, 1831) on Robinson Crusoe Island. Above: Sequence of the song uttered by a male in its territory. Below: call uttered by a male in its territory. The call may be uttered solely or loosely attached initially/finally to the song. Tape recordings were carried out with a DAT-Recorder (Sony; Type HD-S100) with external microphone and wind shield. Illustration bases on the program AVISOFT-SONAGRAPH PRO; program levels are: N=256, F=100, O=75, KHZ=16.

The sequence (Fig. 1, above) is composed of about 50 syllables. Every syllable is built up by one higher and one lower element. The temporal rate of syllables stays very stable throughout the whole sequence (1 syllable per 0.05 sec.). However, frequency range and amplitude of syllables vary during the song, clearly falling towards the end of the sequence. The song generally is very variable: it may continue for longer time durations than shown in Figure 1, repeatedly showing a wave-like structure of slightly falling and rising in pitch. The song reaches extremely high frequency levels. Therefore this firecrown belongs to the few bird species that have voices surpassing the mark of 8 kHz. BERGMANN & HELB (1982) state that this is normally the case with very small birds of low weight. This corresponds to the weight of *Sephanoides fernandensis* (♂ = 10.9 g; ♀ = 7.4 g according to MEZA 1989). The call (Fig. 1, below) is illustrated separately from the song in this case. Although it may be attached to the latter in some cases, it represents an independent feature. It is characterised by two horizontal elements of two frequency ranges (lower element on 5-5.5 and higher on 6.8-7.3 kHz). These elements function as connective structures throughout most of the call, although they end before the last vertical element. The vertical elements cover wide frequency ranges from at least 3.5 up to 8 kHz, without being split up in a higher and a lower part. At the end of the call (1.1 to 1.5 on the time scale) four elements form a unit. The temporal rating of the vertical elements in the call is slower than that of the song, about half of the speed with one element being uttered per 0.1 seconds. The lower temporal rate leads to a more defined structure of single elements and the overall unit than in the song.

The illustrated vocalisations probably have the function of marking the territory and warning competitors not to enter the area of flower agglomerations, as concluded from observations at flowering *Dendroseris* and *Eucalyptus* plants (pres. obs. in 1994 & 2001). Probably the described vocalisations can also have the function of signalising presence to potential partners. The structure of elements, and the pauses between them, turned out to be different in song and call. This is an indication that their functions may differ, even if sometimes uttered one after another. However, yet such functional differences have not been cleared up. Both territorial vocalisation types of *S. fernandensis* are similar in being piercing and loud. They should be identifiable on basis of the presented sonagrams, even by persons not familiar with this species. The field observations showed song/call audibility over a relatively long distance. This may be an evolutionary adaptation of the Juan Fernandez Firecrown to the harsh island conditions and counteract the generally reduced audibility through strong oceanic winds (cf. Hahn & Mattes 2000). Mechanisms behind this may be the wide frequency range of both song and call. The quick repetition of well defined elements additionally contributes to an intensive sounding, heard even over long distances. Field comparisons of audibility to its nearest relative, the Green-backed Firecrown (Colwell 1989; Roy et al. 1998), showed larger distances for endemic Juan Fernandez Firecrowns. Green-backed generally seem to use higher frequencies and temporal ratings (cf. Egli 2002) but a less extended frequency range, and therefore are not heard as far as Juan Fernandez Firecrowns. In turn, the invasive Green-backed fly more and longer distances than Juan Fernandez Firecrowns, and thus compensate this vocal disadvantage through their higher mobility.

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MERZ, B. (ed.) 2006. Phylogeny, Taxonomy, and Biology of Tephritoid flies (Diptera, Tephritoidea). Proceedings of the 3rd Tephritoid Taxonomist's Meeting, Geneva, 19-24. July 2004. Instrumenta Biodiversitatis **7**, 274 pp. ISBN 2-88139-012-9. Price CHF 100.00.

This interesting soft-cover book contains the Proceedings of the 3rd Tephritoid Taxonomist's (sic) Meeting and is the second published volume from this series of conferences. The results of the first and second meetings held in 1998 and 2000, respectively, have also been published (ALUJA & NORRBOM 1999; FREIDBERG 2006). For the third conference the theme was expanded to include researchers working with other families of the superfamily Tephritoidea. In the present proceedings there are 11 articles by 18 authors from eight different countries. Four families, as well as the tephritid subfamily Tachiniscinae, are examined, contributing to the taxonomy and phylogeny (8 articles), biology (1 article), faunistics (1 article) and morphology (1 article) of the Tephritoidea. As stated in its introduction, this volume reflects the high productivity of tephritid workers, the international cooperation among many different laboratories and covers taxa from all biogeographic regions of the world. This well bound book is published by the Muséum d'histoire naturelle, Genève, on glossy paper with excellent black and white line drawings, including many superb habitus illustrations and photographs.

The first contribution revises the eastern Asian and Papuan species of *Herina* of the Ulidiidae (E.P. Kameneva), with the description of 10 new species and the first species-level key from this region. The second paper proposes a classification of the bizarre head structures (appendages, tubercles, stalks, antlers, etc.) that occur in the acalyptrate Diptera (A.E. Whittington), with special emphasis on the extreme head morphology of the Plastotephritinae (Platystomatidae). In the subsequent contribution, the European fossil specimens from the families Pallopteridae, Ulidiidae and Tephritidae are reviewed (G. Gentilini, V.A. Korneyev & E.P. Kameneva), with the description of a new genus and two new species. The next paper revises the genera and species of the Tachiniscinae, treated here as a subfamily of Tephritidae (V.A. Korneyev & A.L. Norrbom). Two new genera and two new species are described; a key to genera and a cladistic analysis are included in this thorough study. The remaining contributions deal exclusively with the more typical tephritids. The fifth article analyses the phylogeny of the subtribe Pelmatopina, an odd group of stalk-eyed tephritids (X.-I. Chen & X.-J. Wang). In a contribution toward resolving the classification of the Dacini, 10 subgenera and 67 species groups of *Dacus* are proposed (D.L. Hancock & R.A.I. Drew), based on an analysis of 32 morphological characters and includes 14 new generic synonymies and a key to subgenera. The following article describes the 3rd instar larva and biology of one of the most enigmatic Palaearctic tephritids, *Malica caraganae* (S.V. & V.A. Korneyev). The eighth contribution describes three new species of *Gymnocarena* (A.L. Norrbom), extending the distribution of this New World genus to Costa Rica. The next article describes a new Afrotropical genus and three new species of the Schistopterini (I. Zonstein & A. Freidberg). The book finishes with two articles on the island faunas of Tephritidae. In the first article, a checklist of 16 species from the Madeiran archipelago is presented (J.T. Smit), including host plant records, ecology and island records. The second article analyses the phylogeny of the Hawaiian tephritids based on mtDNA (J.M. Brown, M. Todd-Thompson, A. McCord, A. O'Brien & B. O'Fallon) and postulates that the 25 endemic species are the result of a single colonization event.

In summary, this book is a stimulating collection of articles covering a large aspect of the Tephritoidea. It has been very carefully edited and the illustrations are all of high quality. This book is not only essential for all tephritoid taxonomists', but will appeal to workers in all aspects of fruit fly research and in the fields of morphology, sexual selection, evolution, biogeography and ecology. The next tephritid taxonomist's meeting is planned for 2008 and I look forward to the subsequent proceedings volume and the excellent reputation that has been developed from the previous two books.

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A New Species of Living Peccary (Mammalia: Tayassuidae) from the Brazilian Amazon

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Abstract. Here we report on the existence of a new species of even-toed ungulate in the Brazilian Amazon, which we name *Pecari maximus*, the giant peccary. It represents the largest of living peccary species. One complete mitochondrial D-loop and two nuclear SINE PRE-1 DNA sequences of giant peccary compared with that of the sympatric and morphologically most similar collared peccary (*Pecari tajacu*) support full species status. The divergence time is estimated at 1.0–1.2 million years before present. In contrast to other peccaries, which are gregarious and range semi-nomadically in large home ranges, giant peccaries appear to live in family groups containing only a pair of adults, with or without 1–2 offspring. In view of recent developments in the interfluves where it lives and due to its limited distribution, we consider the giant peccary endangered.

Keywords. New species, Artiodactyla, Tayassuidae, Pecari maximus, giant peccary, Brazilian Amazon.

1. INTRODUCTION

Until recently only three extant species in the New World Artiodactyla family Tayassuidae (peccaries) were known to science, belonging to three genera (GRUBB 2005): the collared peccary *Pecari tajacu* (Linnaeus 1758), the white-lipped peccary *Tayassu pecari* (Link 1795), and the Chacoan peccary *Catagonus wagneri* (Rusconi 1930). A living population of the latter which was thought to have gone extinct was discovered in 1974 in the Chaco region on the borders of Bolivia, Paraguay and Argentina (WETZEL et al. 1975). During transect surveys of megafauna and fruits conducted in January 2000 in the Rio Aripuanã basin, the first author saw a group of three peccaries, not belonging to any of the known peccary species. Since then, the first author has had several encounters with such peccaries and collected some basic ecological and behavioural data. In March 2003, the first two authors succeeded in filming a group of four such peccaries and collecting zoological material from game brought into the village of Arauazinho.

2. DESCRIPTION OF SPECIES

Class Mammalia
Order Artiodactyla
Family Tayassuidae Palmer, 1897
Genus *Pecari* Reichenbach, 1835

Pecari maximus sp. nov. (Figs. 1–3)

Material. Five skins in the possession of hunters along the lower Rio Aripuanã and a complete skull without exact locality data obtained from them (MR316); an incomplete skull with skin (MR315) from an adult specimen killed in December 2003 along the Rio Arauazinho; a complete skull (INPA4272) from an adult male killed by locals on March 12, 2003, along the left bank of the Rio Aripuanã near the settlement of Arauazinho. Several skulls and mandible parts of all three peccary species occurring in the area were examined as found in the kitchen middens of some local communities.

Diagnosis and discussion. A species of *Pecari* differing from the only other known species in this genus, *Pecari tajacu*, in being much larger but less robust, with much longer legs and a proportionally small head only slightly

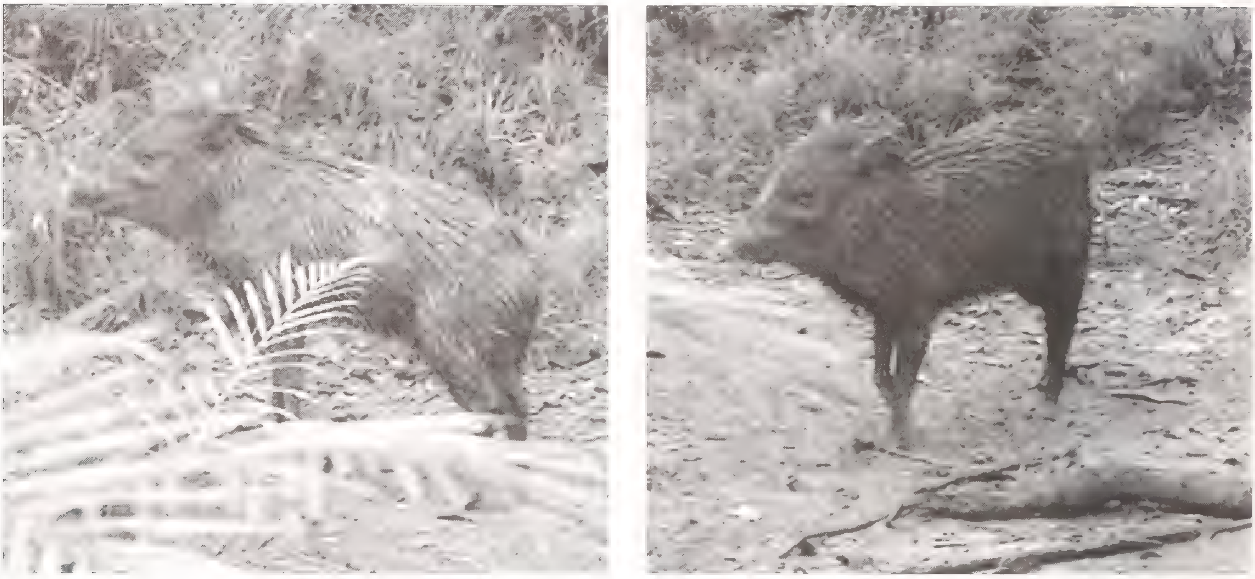

Fig. 1. Wild giant peccary *Pecari maximus* sp. nov. visiting a pond in the middle of continuous high rain forest; **a.** and **b.** show two different adult individuals belonging to the same family of four giant peccaries (Copyright NDR Naturfilm/Roland Gockel).

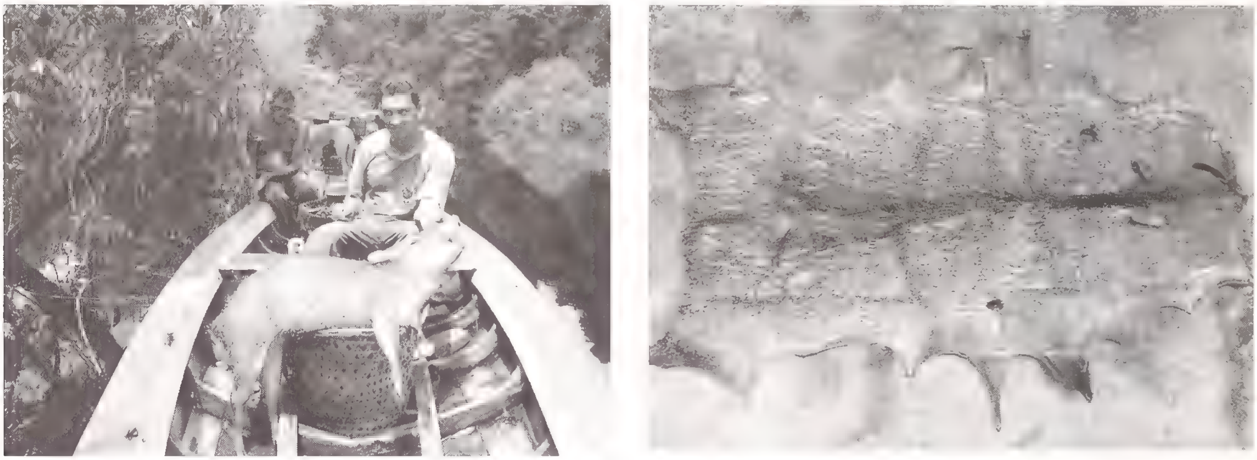

Fig. 2. **a.** (left) Hunters with freshly killed adult male specimen of *Pecari maximus.* The skull of this individual was saved and is here designated as the holotype (INPA4272). (Copyright by Frieder Salm); **b.** (right) Skin of *Pecari maximus* paratype specimen MR315, lacking even a faint collar.

bigger than that of *Pecari tajacu.* Most of the body thinly bristle-haired, overall colour brown mixed with dirty white, a black mid-dorsal mane running from between the ears as far as the rudimentary tail. Ears small and whitish at distal surface. Nasal disc pinkish, relatively small and soft. Collar running over the shoulders very faint, dirty white, or absent (Figs. 1 and 2). Whitish, thinly haired circum-ocular rings (Fig. 1). Distinguished from all other peccary species by its larger size; thin fur; proportionally longer legs giving it a more gracious general appearance; proportionally smaller head - skull length one fifth of total body length in *Pecari maximus*, one quarter in *Pecari tajacu* and *Tayassu pecari* (Woodburne 1968), and nearly one third in *Catagonus wagneri* (Wetzel 1977; Wright 1989); less developed nasal disc; smaller ears. The new species is assigned to the genus *Pecari*, because it possesses a number of traits – in particular cranial features (Fig. 3 and Table 1) – in common with sympatric *Pecari tajacu*, from which it differs by its much larger size and weight (40–50 versus 22 kg), less stocky and longer-legged general appearance, thin, grizzled brown and white fur (instead of thick, dense, strongly speckled dark blackish-grey fur), blacker on the limbs and along the dorsal crest, and a very poorly expressed, sometimes absent, dirty white instead of strikingly contrasting bright white collar passing across the chest from shoulder to shoulder (Bod-

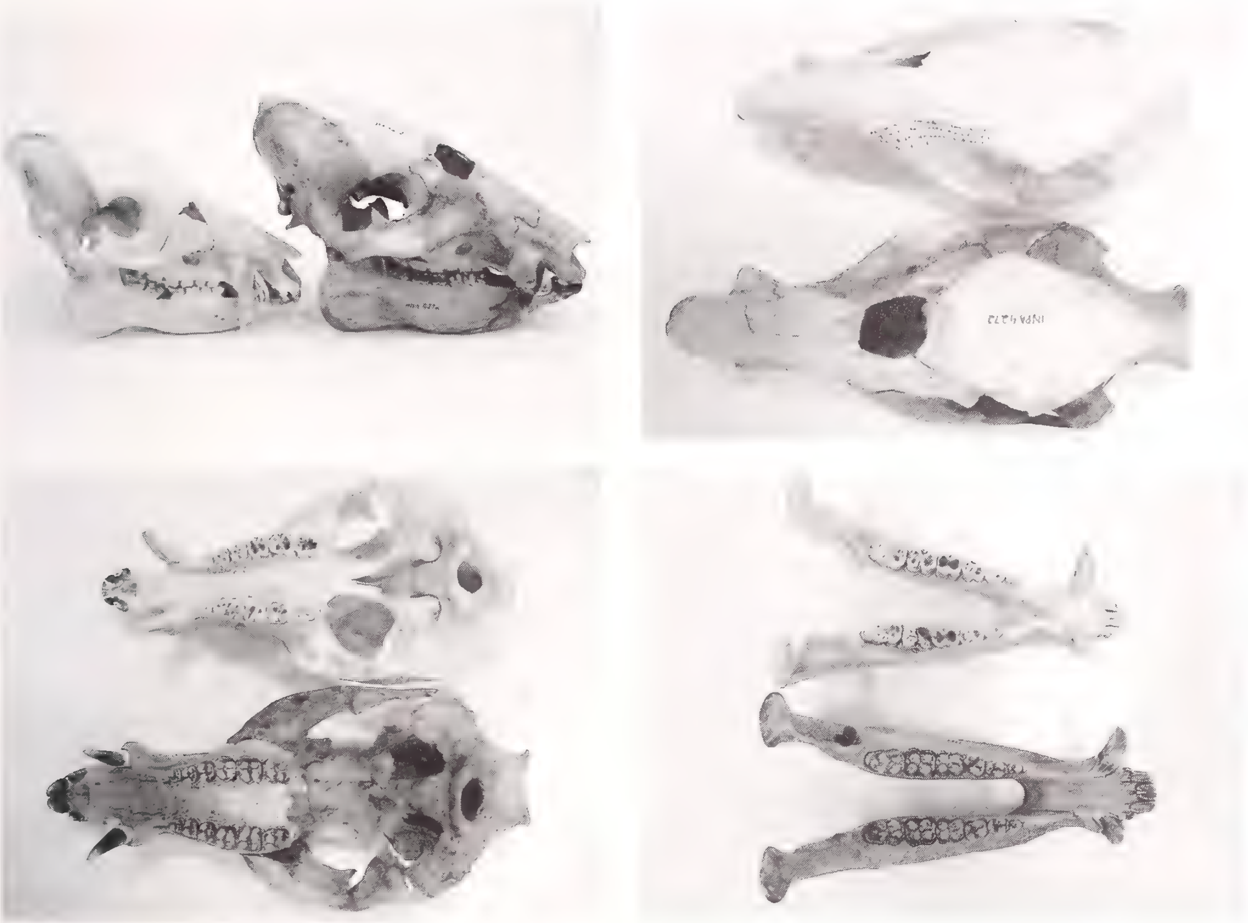

Fig. 3. **a.** Lateral view of the complete skulls of an adult male *Pecari tajacu* from Rio Demeni (INPA283) (left) and an adult male *Pecari maximus* from Rio Aripuanã (holotype INPA4272) (right). **b.** Dorsal view of the same skulls, *Pecari tajacu* (top), *Pecari maximus* (bottom). **c.** Ventral view of the crania of the same skulls (in same arrangement). **d**. Dorsal view of mandibles of the same skulls (in same arrangement).

Mer & Sowls 1993; Grubb & Groves 1993). Distinguished from *Tayassu pecari*, with which it is also sympatric, by its larger body size and weight (40–50 vs. 28 kg), and grizzled-brown thin fur instead of thick, long, evenly coloured blackish brown fur becoming grizzled or light-coloured only in the pectoral and inguinal regions. The forelimbs and legs are only distally black, while they are grizzled black and tan on the lateral and hind surfaces of the forelimbs in *Tayassu pecari* (Grubb & Groves 1993; March 1993). In contrast to the general blackish brown body colour, the chin, cheeks and sides of the muzzle are white or yellowish-white in white-lipped peccaries. Distinguished from *Catagonus wagneri*, with which it is allopatric, by its larger body size and weight (40–50 vs. 29–38 kg), grizzled-brown thin fur with or without a faint dirty white collar instead of brownish-grey thick fur with a distinct bright white collar (Wetzel 1977; Wright 1989; Grubb & Groves 1993).

Overall, the cranium of *Pecari maximus* seems more related to that of *Pecari tajacu* than that of *Tayassu pecari* or *Catagonus wagneri*, but it differs in the following characters: it is clearly longer, wider and more robust; the frontal bone between the postorbital processes is wider; the rostrum behind the canines is wider, the dorsal surface is broader and flatter; the canine buttresses are larger; and the canines are more pointed with sharper edges. Comparing the cranial morphometrics of *Pecari maximus* with *Pecari tajacu* from Brazil (i.e., INPA283, MR317, MR318), where the species appears to grow bigger, especially where it is sympatric with *Pecari maximus*, it may be noted that breadth measurements in general differ more significantly between the species than length measurements. For example, length of cranium, mandible, and mandibular diastema do not show much difference, whereas breadth across zygomatic arches and between postorbital processes of frontals are much greater in *Pecari maxi-*

Table 1. Cranial and dental measurements [mm] of *Pecari maximus* sp. nov., *Pecari tajacu* and *Tayassu pecari*, following WOODBURNE (1968). *Pecari maximus* is represented by the holotype INPA4272 and the paratypes MR316 and MR315 (incomplete skull); *Pecari tajacu* is represented by INPA283, an adult male from Rio Demeni, MR317, an adult male (head-body length: 1100 mm) from Rio Arauazinho, and MR318, an adult female (head-body length: 1080 mm) from Rio Arauazinho. The second column of measurements of *Pecari tajacu* is of specimens collected outside Brazil in the northern part of the species' range where individuals are on average smaller than those from central Amazonia; these and the measurements for *Tayassu pecari* were taken from WOODBURNE (1968)

Cranium	***P. maximus* sp. nov. (N=3)**	***P. tajacu* (N=3)**	***P. tajacu* mean (N=71)**	***T. pecari* mean (N=41)**
Length of cranium (= length anterior tip of I^1 to rear of condyles)	262;260;---	230;255;258	202	235
Length of diastema from C to P^2 (distance from rear edge of alveolus of C)	31;30;---	21;25;26	18	26
Width between alveoli of P^2	18;20;---	14;17;16	18	21
Width between alveoli of M^3	20;19;19	18;18;18	18	20
Least width of rostrum behind canines	39,5;40;---	35;35;35	31	53
Height from condyles to nuchal crest	85;85;85	73;80;80	81	99
Breadth across zygomatic arches	119;120;119	104;110;95	101	118
Breadth between postorbital processes of frontals	88;88;89	78;78;71	73	92
Mandible				
Length of mandible (= length from I^1 to rear of condyles)	185;180;182	165;170;173	162	198
Length of diastema from C to P_2	40;35;36	31;37;37	25	34
Depth from tip of coronoid process to ventral angle	88;85;84	73;82;77	75	93
Depth below P_2	36;39;40	32;40;37	32	36
Depth below rear of M_3	45;45;45	32;33;35	34	41
Width between alveoli of P_2	20;25;24	20;22;21	22	26
Width between alveoli of M_3	25;25;24	26;27;26	27	31
Width between condyles	49;55;---	52;47;48	49	58
Length from P_2 to M_3	65;68;68	63;62;64	69	85

mus. The width between alveoli of M^3 is slightly greater in *Pecari maximus* implying a differently shaped palate. Whereas the depth below P_2 is the same in the two species, the depth below rear of M_3 is much greater in *Pecari maximus*, so that the lower jaw deepens posteriorly (for a more detailed comparison, see Table 1).

GRUBB (2005) lists the following 19 synonyms for *Pecari tajacu*: *angulatus*, *bangsi*, *caitetu*, *crassus*, *crusnigrum*, *humeralis*, *macrocephalus*, *minor*, *modestus*, *nanus*, *nelsoni*, *niger*, *nigrescens*, *patira*, *sonoriensis*, *tajassu*, *torquatus*, *torvus*, *yucatanensis*. Three subspecies groups have been differentiated in the past – the grey forms ('*angulatus*' group) from Central America (Texas, Mexico and Honduras), the blackish forms with poorly expressed collar and dorsal stripe ('*patira*' group) from the Guianas, Colombia, Ecuador and Panama, and the buff forms with clearly marked pale collar and black dorsal stripe from South America (the nominate '*tajacu*' group). The synonyms of the South American forms apply to specimens

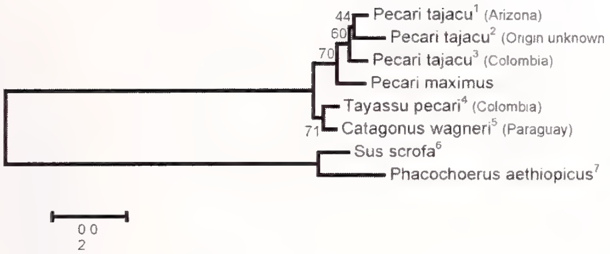
44
60
70
71
Pecari tajacu¹ (Arizona)
Pecari tajacu² (Origin unknown
Pecari tajacu³ (Colombia)
Pecari maximus
Tayassu pecari⁴ (Colombia)
Catagonus wagneri⁵ (Paraguay)
Sus scrofa⁶
Phacochoerus aethiopicus⁷
0 0
2

Fig. 4. Neighbour-joining tree of combined nuclear PRE-1 P27 and P642 sequences. The tree was constructed with MEGA3 (KUMAR et al. 2004), assuming the TN93 Gamma model (shape parameter alpha = 0.6). Bootstrap values (10,000 replicates) are indicated on branches. Geographic origins are mentioned between brackets. The superscripts refer to Genbank accession numbers. 1: AY546529/AY726778, 2: AB000378/379, 3: AY546532/AY726779, 4: AY546528/31, 5: AY546527/30, 6: AB000365/370, 7: AB000377/678.

collected in Colombia, Ecuador and the Guianas, areas north of the Amazon River, being geographically too distant from the range of the new taxon, *Pecari maximus*, for these synonyms to be taken into account. Linnaeus' name *Sus tajacu* is based on the tajacu of Marcgraf (GRUBB 2005), from the State of Pernambuco, Brazil, a region that is not considered part of Amazonia.

Measurements. Five skins from hunters along the lower Rio Aripuanã were measured, total length 120, 127, 133, 135 and 137 cm. Collar when present 35 cm. Nasal disc 5.3 x 4.0 cm. Mane bristles 10.5–12.0 cm, proximally with 2–3 white bands at the lower half and 3 brown bands, distally with 3 white and 4 brown bands, the white bands only on lower half of bristles. Bristles to the side of the mane 6–7 cm, the dorsal ones with 3 whitish bands, the more ventral ones 4.7 cm, with only 2 whitish bands. Collar bristles 3.6–4.3 cm, with or without 1–2 white bands on distal part. The upper legs have black, fine, non-annulated, 4.0 cm long hairs. Belly almost naked, the hairs vaguely banded or only with one whitish band at the base. Bristles on nape 8.5 cm, with one whitish band only. Proximal bristles 8.0 cm, with one whitish narrow band only. Based on film and photo material of wild animals we estimated the following average measurements for adults: total body length 127 cm; ear length 13 cm; shoulder height 85 cm. Body weight was not taken but according to local hunters ranges from 40–50 kg. Mean skull length 261 mm, mean mandible length 182 mm. For additional skull measurements of *Pecari maximus* n.sp., *P. tajacu* and *Tayassu pecari* and definitions of measurements see Table 1.

Type Material. Holotype: INPA4272 (Mammal Collection of the National Institute for Amazon Research, Manaus, Amazonas, Brazil): complete cranium and mandible of an adult male (Fig. 3), killed for food by a local hunter, Luís Corrêa Bastos, on March 12, 2003, along the left bank of the Rio Aripuanã near the settlement of Arauazinho. Figure 2a shows the freshly hunted animal from which only the skull could be saved that is here designed as the holotype.

Paratypes: MR315, an incomplete skull with skin (Fig. 2b), obtained from hunters who had killed the animal in December 2003 along the Rio Arauazinho; MR316, a complete cranium and mandible collected from hunters living along the lower Rio Aripuanã, but lacking exact locality data (both paratype specimens kept by the first author).

Type locality. Left bank of the Rio Aripuanã, close to the settlement of Arauazinho, situated at the mouth of the Rio Arauazinho, a left bank tributary of the lower Rio Aripuanã, State of Amazonas, Brazil (06°16′94′′S, 60°20′87′′W).

Etymology. The name is Latin meaning 'the largest', referring to the size of the new species that is the largest among living peccaries. The gender is masculine.

Vernacular name. *Pecari maximus* is locally known as 'caitetú-mundè'. Locals claim that in the Tupi-Indian tongue (*lingua geral*) it means "the collared peccary that is bigger and goes in pairs". This allows them to distinguish it from *Pecari tajacu* commonly known as 'caitetú-de-bando' ("the collared peccary that goes in herds").

3. PHYLOGENY

Mitochondrial cytochrome *b* (THEIMER & KEIM 1998), control region and 12S r RNA sequences, and nuclear SINE PRE-1 sequences (GONGORA & MORAN 2005) indicate that *Tayassu pecari* and *Catagonus wagneri* are more closely related to each other than to *Pecari tajacu.* A complete mitochondrial D-loop sequence (1383 bp) and two nuclear SINE PRE-1 sequences (P27, 322 bp and P642, 386 bp) (homologous sequences described in SULANDARI et al. [1997] and GONGORA & MORAN [2005]) from our skin sample (MR315) support the status of the new peccary species as belonging to the genus *Pecari*, closely related to *Pecari tajacu.* Sequences are deposited in GenBank under the accession numbers: DQ009006, DQ016371 and DQ016372. Net maximum likelihood (TN93) sequence divergence with *Pecari tajacu* is 2.0 % (Colombia, GenBank accession numbers: AY546522, AF276938) and 1.1 % (GenBank accession numbers: AY26778-79, AY546529/32, AB000378-79), respectively. For the D-loop it is of the same order as observed between the European and Asian pig (1.7 %) (KIM et al. 2002), for which the divergence time has been estimated

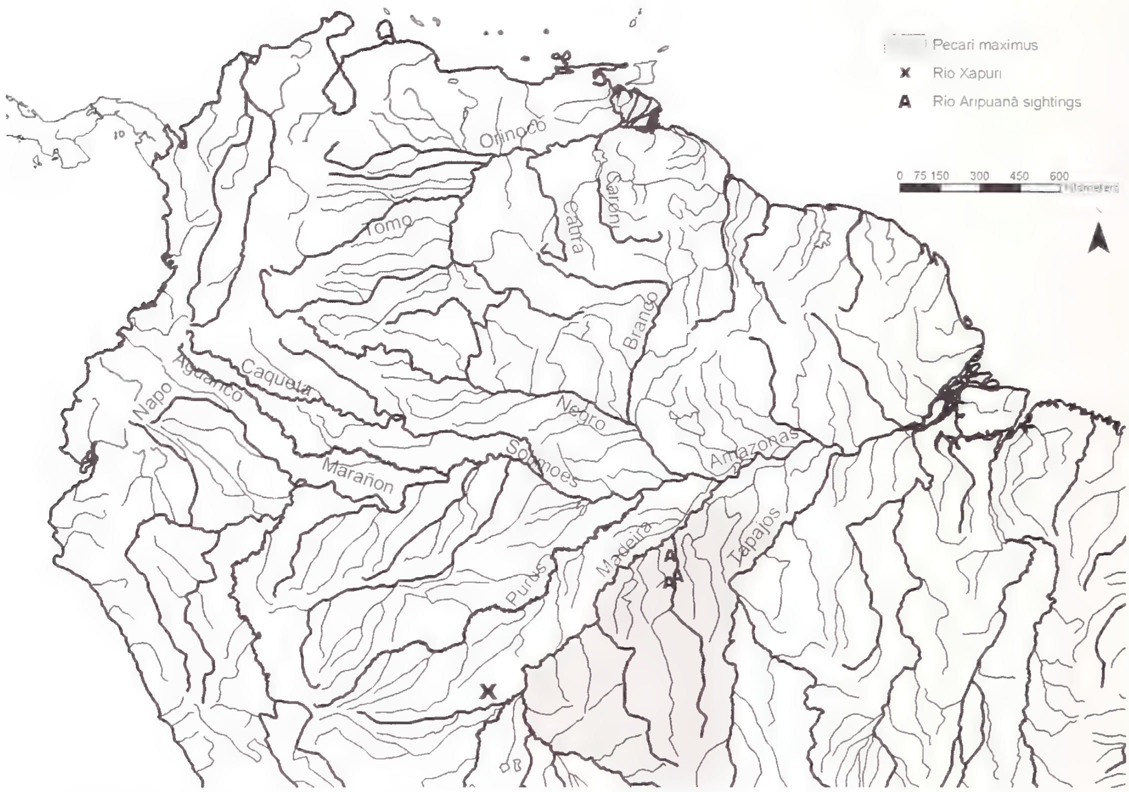
Pecari maximus
X Rio Xapuri
A Rio Aripuanã sightings
0 75 150 300 450 600
Kilometers
Orinoco
Tomo
Caroni
Caura
Branco
Napo
Aguarico
Caqueta
Negro
Marañon
Solimoes
Amazonas
Tapajos
Madeira
Purus

Fig. 5. Assumed distribution (shaded) of *Pecari maximus* sp. nov. in the Brazilian Amazon, based on sightings in the wild and interviews with locals. A question-mark indicates the Rio Xapurí where an American rubber cutter working in the area from 1906–1916 described game that is similar to the giant peccary both in general appearance and behaviour (Yungjohann 2003).

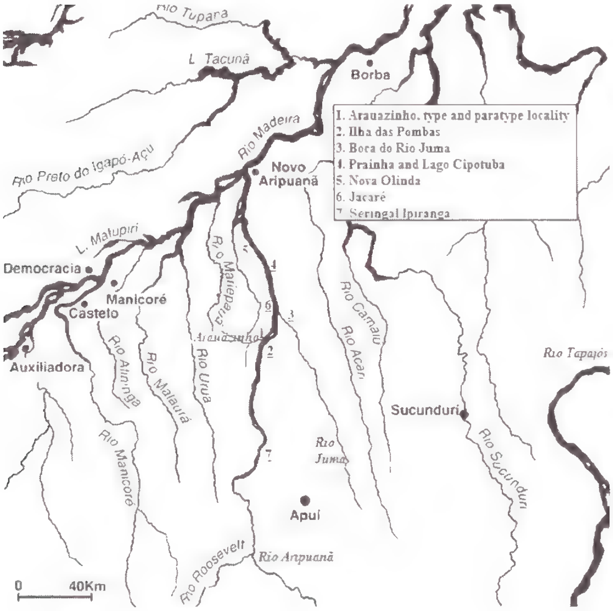
Rio Tupara
L. Tacunã
Borba
Rio Madeira
Rio Preto do Igapó-Açu
Novo Aripuanã
1. Arauazinho, type and paratype locality
2. Ilha das Pombas
3. Boca do Rio Juma
4. Prainha and Lago Cipotuba
5. Nova Olinda
6. Jacaré
7. Seringal Ipiranga
L. Matupiri
Democracia
Manicoré
Castelo
Auxiliadora
Rio Atininga
Rio Mataurá
Rio Uruá
Rio Mariepaua
Rio Camaiu
Rio Acari
Rio Tapajós
Sucunduri
Rio Sucunduri
Rio Juma
Rio Manicoré
Apuí
Rio Roosevelt
Rio Aripuanã
0 40Km

Fig. 6. Collecting and sighting localities for *Pecari maximus* sp. nov. along the Rio Aripuanã.

at 860,000 years before present on account of near-complete mtDNA genome sequences (Kijas & Andersson 2001). This indicates a divergence time between *Pecari tajacu* and *Pecari maximus* of 1.0 million years before present. The combined SINE PRE-1 sequences indicate a similar divergence time of 1.2 million years before present assuming a mutation rate of 4.6×10^{-9} per year per site (Sulandari et al. 1997). Figure 4 shows a neighbour-joining tree including all known Tayassuidae species.

4. DISTRIBUTION, ECOLOGY AND CONSERVATION STATUS

Distribution

The larger geographical distribution of the giant peccary is thought to be the interfluve delineated by the Rio Madeira in the west, the Rio Tapajós-Juruena in the east, the Rio Amazonas in the north and the Rio Guaporé in the south (Fig. 5). Since *Pecari maximus* appears to be confined to *terra firme* rainforest habitat we assume that its real distribution is much smaller and does not extend into the northern part of the Rios Madeira/Tapajós interfluve, where there are many open savannahs and extensive floodplains. We have observed the species in the wild only along both banks of the Rio Aripuanã (Fig. 6); it swims well (pers. obs.). The species might also occur in the upper Rio Madeira, State of Acre (Fig. 5). This assumption is based on the story of an American, John C. Yungjohann, who worked as a rubber cutter in the Rio Xapurí area from 1906–1919, written down in the book "White Gold" (YUNGJOHANN 2003). He describes three types of 'bush pigs'. The description of one of these closely resembles *Pecari maximus*: "there is a great, big one *porcão*, they travel in pairs, and are very lively. They will attack on sight – either you have to be swift and a sure shot or climb a tree". This behaviour – going in pairs and being really aggressive when attacked – is also reported by the hunters along the Rio Aripuanã.

Ecology

Both *Pecari tajacu* and *Tayassu pecari* roam semi-nomadically in a highly variable landscape in noisy, widely spread herds of up to 30, respectively 200 individuals, which stay in permanent contact by loud tooth-clicking. In strong contrast, *Pecari maximus* seems to walk silently through its preferred habitat – dense *terra firme* climax forest – in small family groups that contain only an adult pair with or without 1–2 offspring. *Pecari maximus* appears to perform little or no uprooting, whereas the gregarious peccary species largely forage for subsoil seed shadows, seedlings, roots and tubers. Instead, it has been seen feeding predominantly on freshly fallen fruits and seeds exposed on the forest floor. If this is its predominant foraging technique, its different dietary specialisation might well explain the fact that among the several skull and mandible parts of the three local species combined, the molars of *Pecari maximus* invariably showed a less dramatic wearing pattern. This could reflect its much smaller intake of sand and dirt during feeding. It appears that the larger *Pecari maximus* has abandoned social groupings, group defence and territorial scent marking. Its scent gland is thought to be rudimentary. None of the skins examined emitted the typical peccary scent, suggesting that if any secretory liquid is produced it is scentless, at least for the human nose.

Conservation status

All three peccary species occurring sympatrically in the Rio Aripuanã region are the favourite game of the locals, but only *Pecari maximus* is hunted with dogs since it does not go in herds like the other peccaries which are known to defend themselves fiercely. Although human occupation in this part of the Amazon is presently very low, this situation might soon change. In the Rio Aripuanã region unprecedented illegal extraction of timber and gravel is taking place. Recent road building through the area is intended to connect the town of Manicoré on the right bank of the Rio Madeira with the boomtown of Apuí at the border of the Tenharim Savannah and the State of Mato Grosso, areas of large-scale soybean agriculture. In view of these recent developments, we fear that commercial hunters using trained dogs will focus first on *Pecari maximus* to feed hungry settlers. Taking increasing hunting pressure and the species' limited distribution into account, we consider *Pecari maximus* endangered. We recommend inclusion of this new species in the IUCN Global Red List, based on criterion D (very small or restricted population). Besides the giant peccary, the Rio Aripuanã region is thought to harbour a number of floral and faunal elements new to science. The first author has identified so far a new species of dwarf porcupine, *Coendu roosmalenorum* Voss & da Silva, 2001 (VOSS & DA SILVA 2001), and seven new primate species, four of which are already described (VAN ROOSMALEN et al. 1998; VAN ROOSMALEN et al. 2000; VAN ROOSMALEN et al. 2002; VAN ROOSMALEN & VAN ROOSMALEN 2003). Among these primates, the dwarf marmoset *Callibella humilis,* represents a new genus never collected before. Most surprisingly, not a single area protected by Brazilian environmental law exists in the region. Given the uniqueness of the region in terms of biodiversity and its current status of biological *terra incognita*, we here encourage UNESCO to urge the Brazilian government to declare the entire region a World Heritage Site.

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A new species of the *Creatonotos transiens*-group (Lepidoptera: Arctiidae) from Sulawesi, Indonesia

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Abstract. A new species from Sulawesi (Celebes), *Creatonotos kishidai* Dubatolov & Holloway is described. It is characterized by the presence of a sclerotized spine-bearing band which envelops the aedeagus apex, presence of spining on the juxta, and small peniculi (finger-like processes) at the bases of the transtilla, which are longer than in the widespread Oriental *C. transiens* (Walker, 1855) and shorter than in *C. wilemani* Rothschild, 1933 from the Philippines. The holotype of the new species is deposited in the Siberian Zoological Museum of the Institute of Animal Systematics and Ecology, Novosibirsk, Russia. Study of a topotype of *C. transiens vacillans* (Walker, 1855) showed that it is a senior synonym of *C. t. orientalis* Nakamura, 1976. *C. ananthakrishanani* Kirti et Kaleka, 1999 is synonymized with the nominotypical subspecies of *C. transiens* (Walker, 1855). The lectotype of *C. transiens* (Walker, 1855) is designated in the BMNH collection from "N. India, Kmorah" (misspelling of "Almorah").

Keywords. Tiger-moth, Arctiidae, Arctiinae, *Creatonotos*, *Creatonotos transiens*-group, new species, Sulawesi, Indonesia.

1. INTRODUCTION

The genus *Creatonotos* Hübner, [1819] 1816 consists of a set of unrevised Afrotropical species (GOODGER & WATSON 1995) and seven species from South Asia and neighbouring territories. Two species are distributed throughout the whole Oriental region: *C. transiens* (Walker, 1855) and *C. gangis* (Linnaeus, 1763), the latter reaches its limits in Northern Australia, South Iran and North-Eastern Arabia (1 ♂, 1 ♀, United Arab Emirates, 1 km W Marbad, 25°20'N 56°07'E, 28.III – 5.IV 2006, leg. M. Fibiger & C. Gielis, ex Zoological Institute (St.-Petersburg, Russia) collection). Two species are much more localized within the Oriental Region: *C. fasciatus* (Candèze, 1927) was described from Cambodia, *C. wilemani* (Rothschild, 1933) inhabits the Philippines. To these must now be added *C. kishidai* sp. n. from Sulawesi. Two species are known from Western Arabia: *C. albidior* Wiltshire, 1986 and *C. leucanioides* Holland, 1893. *C. arabicum* (Hampson, 1896) from South-Western Asia has been assigned to a new genus *Creataloum* Dubatolov, 2004. The *Creatonotos* species from Asia fall into two main groups defined by the forewing pattern and male genitalia structure; these could be treated as subgenera. Species of the nominotypical subgenus have light wings with a dark streak along the posterior vein of the cell, and have long needle-like cornuti on the vesica: *C. gangis*, *C. albidior*, *C. leucanioides* and, taking into account the forewing pattern only, *C. fasciatus*. The *C. transiens* group might be referred to subgenus *Phissama* Moore, 1860, the species having forewings without a streak along the posterior vein of the cell, and having short, drawing-pin-like cornuti on the vesica that are sometimes fused into bands.

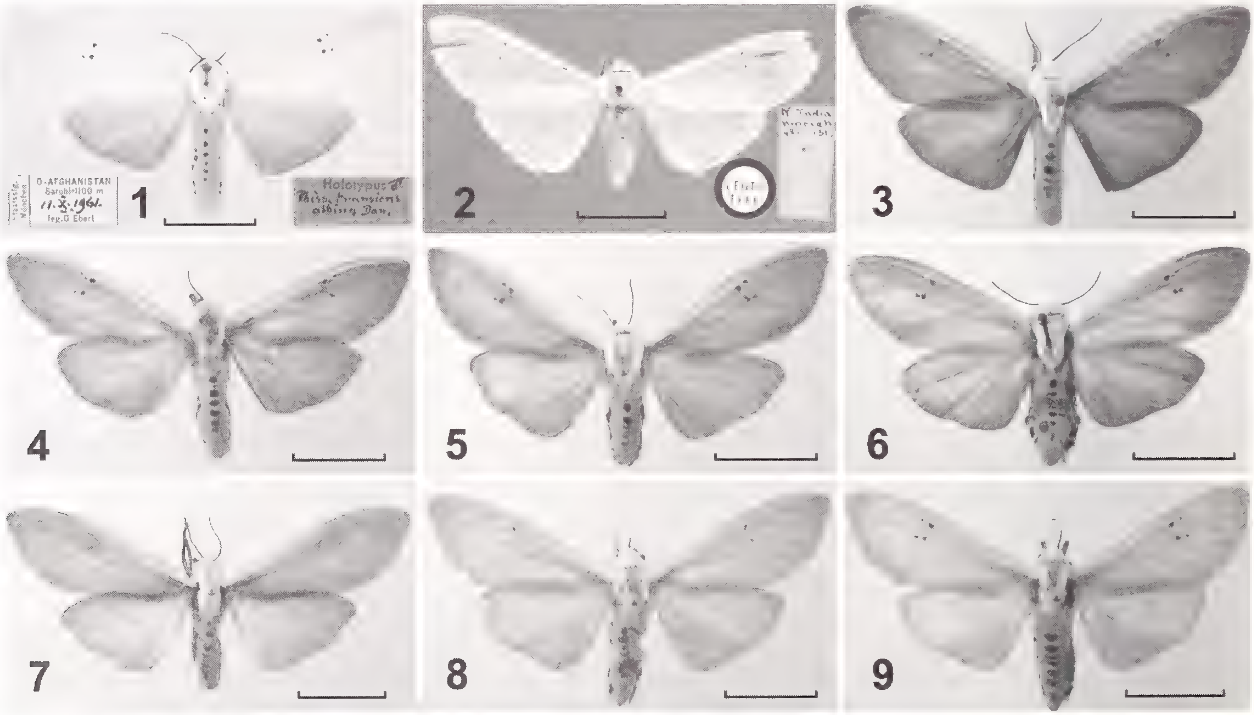
2. TAXONOMY

NAKAMURA (1976) reviewed the latter group and recognised two species. On the basis of male genital structure, he divided *C. transiens* (Walker, 1855) into four subspecies, and described a sibling species, *C. philippinense* Nakamura, 1976, from the Philippines. HOLLOWAY (1988) and INOUE (1988) independently found an older name for the latter, *C. wilemani* Rothschild, 1933, which was originally described as a distinct species. HOLLOWAY (1988) also found that there was a further taxon of this group on the Indonesian island of Sulawesi, but did not describe it at the time. After a careful study of *Creatonotos* specimens kindly sent by Mr Y. Kishida to the collection of Siberian Zoological Museum of the Institute of Animal Systematics and Ecology, Novosibirsk, Russia (SZMN), it became apparent that the new taxon from Sulawesi has several striking characters of the male genitalia that distinguish it from both *C. transiens* and *C. wilemani*. It should therefore be described as a new species.

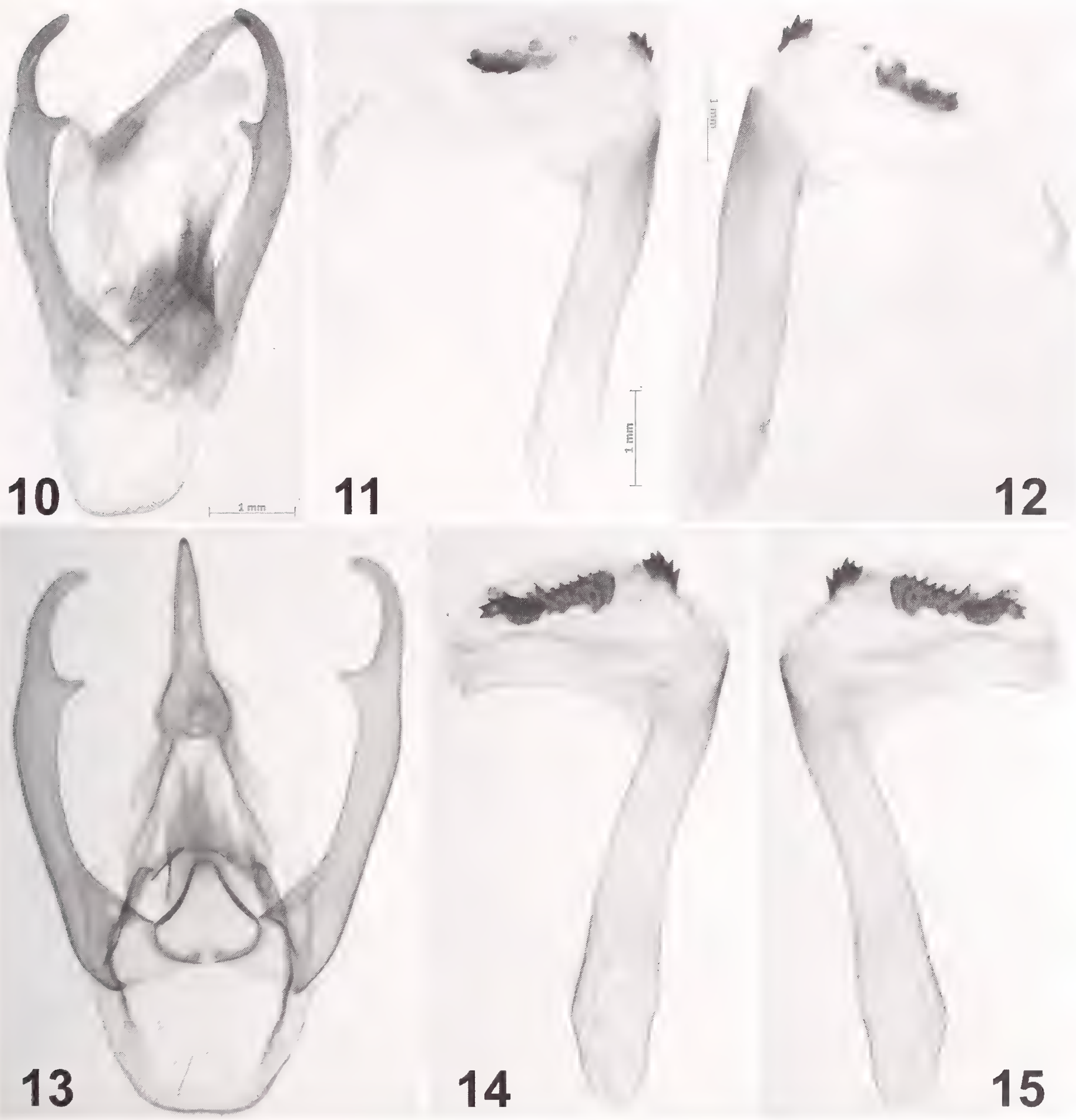
However, a female specimen from Sulawesi was included in the type series of *C. transiens*, along with other females from North India, Sylhet, and East Indies. A lectotype of *C. transiens* has yet to be designated. Hampson (1901) treated a specimen from Sylhet as "type" of *C. transiens*, but neither syntype with these data (from the Sowerby collection) was rediscovered during our investigations. So, there are two female syntype specimens from North India, Almorah, from the Stevens collection, and they belong to the nominotypical *C. transiens* subspecies sensu Nakamura (1976). Therefore, in the interests of stability, one of these females from North India, Almorah (handwritten on the label as "N. India, Kmorah"), is hereby designated as the LECTOTYPE (Fig. 2). Similarly, the type series of *Aloa isabellina* Walker, 1855 included male and female specimens from Sylhet, North India and East Indies. These localities, taken at face value, are shared with *transiens*, but the concept of 'East Indies' is very imprecise and may involve parts of southeast Asia and Indonesia where other races occur; in fact, the type material so labelled for both taxa was from the Archdeacon Clerk collection, and the one syntype of *transiens* located from this source is labelled as from Moulmein in southern Burma (Myanmar). Therefore, in the interests of stability, we designate the Sylhet male specimen of *isabellina* as LECTOTYPE. It is possible that North India and East Indies syntypes of *transiens* were also listed as syntypes of *isabellina*, given that only six syntypes of the taxa together have been located.

The discovery of the new species from Sulawesi led us to review geographic variation in male genitalia for the whole *C. transiens* group. For this, we use the terminology of Nakamura (1976) for the ornamentation of the aedeagus vesica.

First of all, it was found that the male genitalia of a *C. t. vacillans* (Walker, 1855) topotype specimen from Hong Kong do not differ from those of *C. t. orientalis* Nakamura, 1976 from Thailand in the structure of the fused cornuti plate M1-M2-M3-M4-B of Nakamura (1976), the shape of which can vary significantly even in geographically close populations; it differs from *C. t. koni* Miyake, 1909 from Taiwan and South Japan, which has the cornuti plate disrupted into several cornuti M1, M2, M3, M4. Moreover, two continental subspecies, the nominotypical *C. t. transiens* and *C. t. vacillans*, differ only slightly from each other, the former from the Himalayas and India hav-



Figs 1–9. *Creatonotos*, adult moths. **1.** *C. transiens albina*, holotype, Afghanistan, Sarobi, 1100 m, 11.X 1961, G. Ebert leg. **2.** *C. transiens*, lectotype and its labels, "N. India, Kmorah". **3.** *C. t. transiens*, India, E Sikkim, 20 km SE of Ganghtok, Phidim Rain Forest, h = 1600 m, VII 2002, O. Yu. Ammosov leg. **4.** *C. t. vacillans*, Vietnam, Cao Bang, Mt. Pia Oak, h = 1700 m, III 2002, native collector leg. **5.** *C. t. sundana*, Indonesia, Bali, Tamblingan, VI 2004, native collector leg. **6.** *C. t. koni*, Japan, Okinawa, Naha, P. Schmidt leg. **7.** *C. wilemani*, Philippines, Negros Is., Mt. Canlaon, native collector leg. **8–9.** *C. kishidai*, Indonesia, Sulawesi, Tondano, VII 1988, native collector leg. **8.** Holotype. **9.** Paratype. **2.** Female. **1, 3–8.** Males.

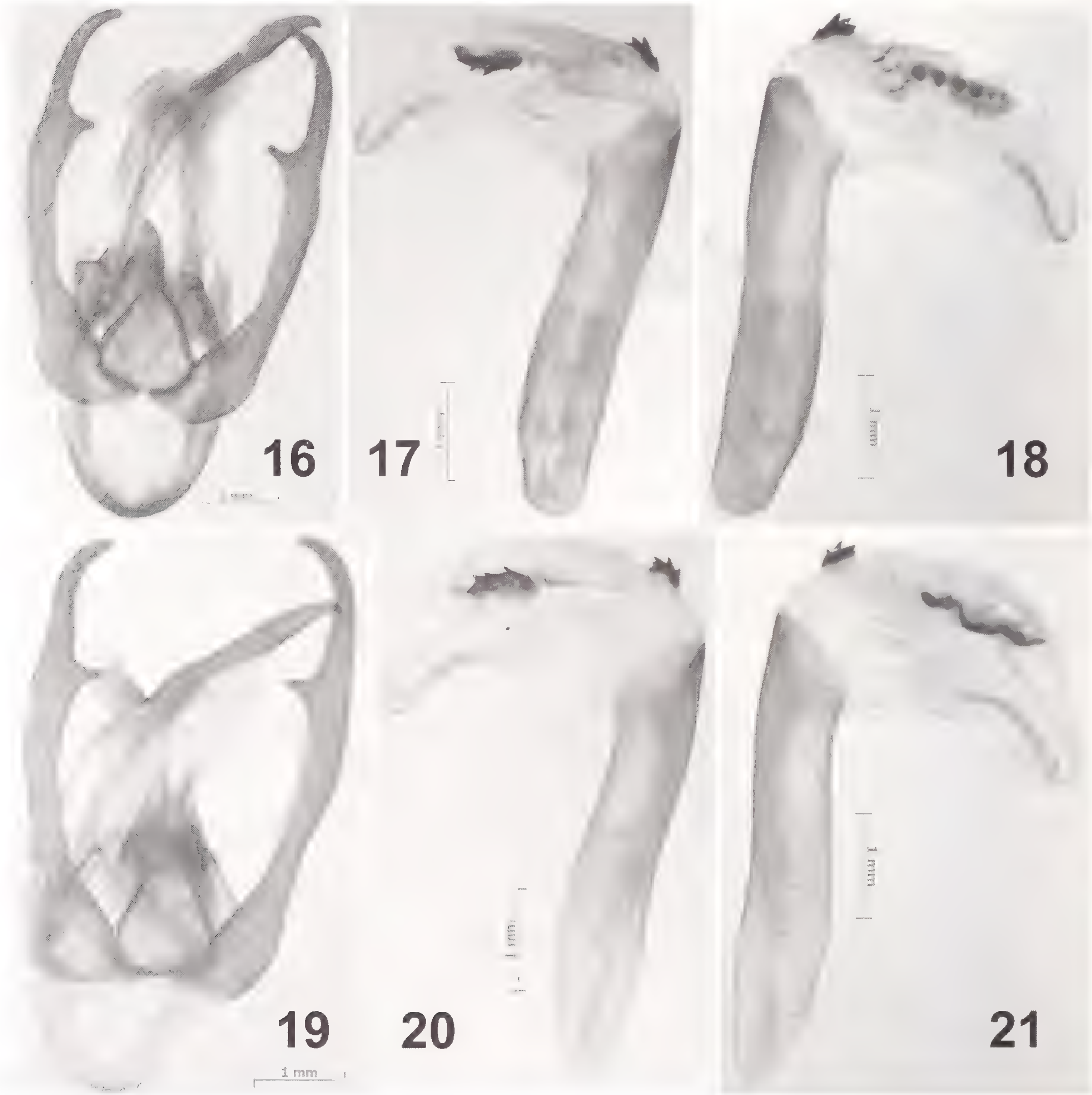


Figs 10–15. Male genitalia of *Creatonotos*. **10–12.** *C. t. transiens*, India, E Sikkim, 20 km SE of Ganghtok, Phidim Rain Forest, h=1600 m, VII 2002, O. Yu. Ammosov leg. **13–15.** *C. t. albina*, Afghanistan, Sarobi, 14.X 1961, G. Ebert leg. **10, 13.** General view. **11, 14.** Aedeagus, left side. **12, 15.** Aedeagus, right side.

ing a more uneven cornuti plate M1-M2-M3-M4-B. So, the list of the *C. transiens*-group taxa is as follows:

***Creatonotos transiens* (Walker, 1855)** (Figs 1–6)

South-East Asia from India to China, South Japan, Borneo and Lombok. Records of *C. transiens* from the Philippines in HOLLOWAY (1976, 1988) are likely to have arisen from misplaced specimens of *C. wilemani* in the series of *C. transiens* in BMNH; these were recognised as misidentified subsequently, and one is the Philippines specimen included amongst those listed by WALKER (1856) in his redescription of *vacillans* (see below). A further search of supplementary drawers has not yielded any Philippines specimens that are definitely *C. transiens*, so this record must be treated as suspect.



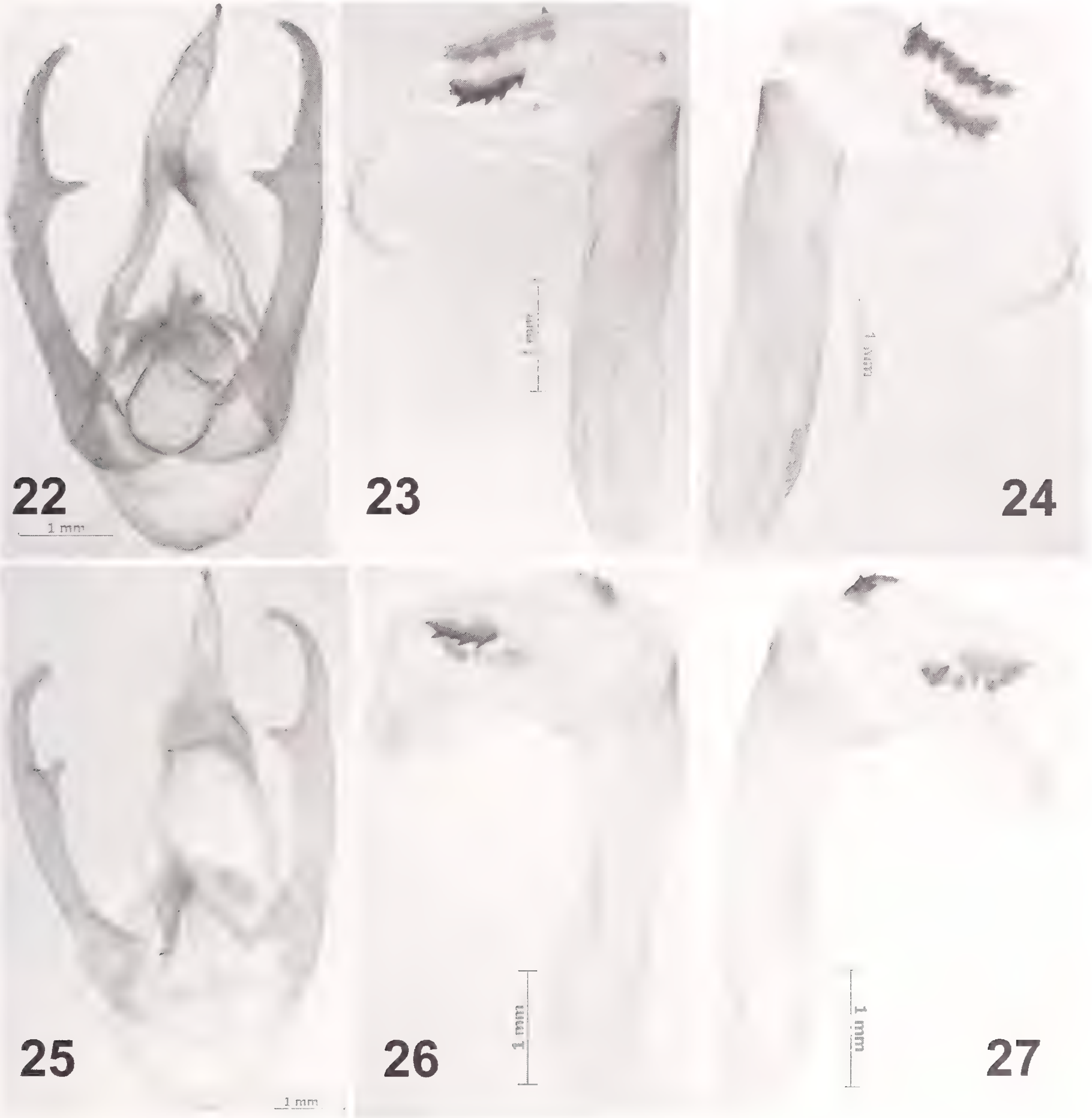
Figs 16–21. Male genitalia of *Creatonotos*. **16–18.** *C. t. vacillans*, Hong Kong, Kan Sui Chan, 31.XII 2005, J. Lee leg. **19–21.** *C. t. vacillans*, Thailand, Chanthaburi Province, Khao-Khitchakut National Park, by light at headwaters, 6.I 2006, O. E. Kosterin leg. **16, 19.** General view. **17, 20.** Aedeagus, left side. **18, 21.** Aedeagus, right side.

C. t. albina (Daniel, 1971); Ann. Naturh. Mus. Wien **75**: 654, t. 1, fig. 5 (*Phissana transiens albina*); type locality: "[O-Afghanistan] … Sarobi" [Paktika: Sarowbi] (Fig. 1).

Afghanistan: Paktika, Nangarhar, Nuristan, Badakhshan (Daniel 1971).

Remarks. According to the original description (Daniel 1971) and the figure of the holotype (Fig. 1), this subspecies has the palest whitish-grey wings in males (forewing being noticeably lighter than hindwings) and white wings in females. Male genitalia were stated by Daniel to be identical with the nominotypical subspecies; however, they are only similar (Figs 13–15). Cornuti patch M1-M2-M3-M4-B of right side of vesica is massive, regular in shape; cornuti patch O is large, like in the nominotypical subspecies.

C. t. transiens (Walker, 1855); List Specimens lepid. Insects Colln. Br. Mus. **3**: 675 (*Spilosoma transiens*); type locality: North India, Almorah, designated here from the lectotype (Figs 2–3).



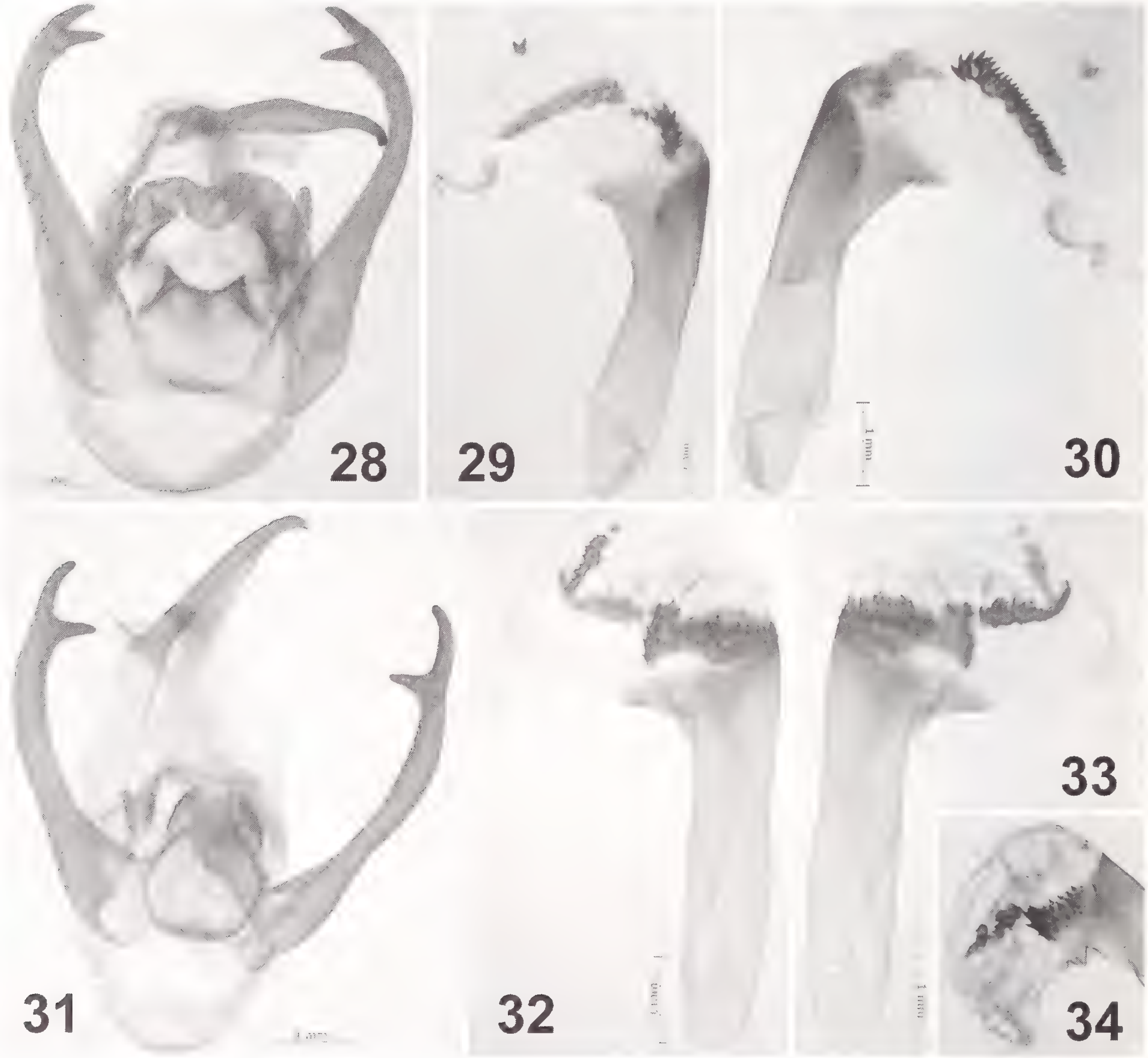
Figs 22–27. Male genitalia of *Creatonotos*. **22–24.** *C. t. sundana*, Indonesia, Mentawai Isl., Siberut Isl., Bojakan, IX 2004, native collector leg. **25–27.** *C. t. koni*, Japan, Okinawa, Taha, P. Schmidt leg. **22, 25.** General view. **23, 26.** Aedeagus, left side. **24, 27.** Aedeagus, right side.

=*Aloa isabellina* Walker, 1855; List Specimens lepid. Insects Colln. Br. Mus. **3**: 705–706; type locality: Sylhet, designated here from the lectotype.

=*Creatonotos ananthakrishanani* Kirti et Kaleka, 1999, **syn. nov.**; Entomon **24** (2): 137–140, figs 1–11; type locality: "Uttar Pradesh: Mussorrie".

India, North Pakistan (a photo of a male specimen from the Indus Canyon, 50 km E of Peshawar in Mr. V. Gurko's collection (Tchernovtsy, Ukraine) has been studied).

Remarks. *C. ananthakrishanani* Kirti et Kaleka, 1999 was described from the North-West Himalayas, Mussorrie, on the basis of differences in wing venation from *C. transiens* and misinterpreted minute differences in male genitalia. Moreover, the authors mistakenly considered there to be two cornuti groups in *C. transiens* and three groups in *C. ananthakrishanani* (Fig. 36), but they never everted vesicas in both taxa. Presence of three cornuti groups is characteristic for the whole *C. transiens*-complex. The specific status of *C. ananthakrishanani* is therefore unjustified. The nominotypical subspecies vary from the darkest



Figs 28–34. Male genitalia of *Creatonotos*. **28–30.** *C. wilemani*, Philippines, Negros Is., Mt. Canlaon, native collector leg. **31–33.** *C. kishidai*, holotype, Indonesia, Sulawesi, Tondano, VII 1988, native collector leg. **34.** – *C. kishidai*, paratype, Indonesia, Celebes [Sulawesi], Loda, Paloe, 4000', V 1937, J. P. A. Kalis (Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany). **28, 31.** General view. **29, 32, 34.** Aedeagus, left side. **30, 33.** Aedeagus, right side.

brown forewings in the specimens from Sikkim to the pale brown forewings in the specimens from North India and North Pakistan, whilst in male genitalia (Figs 10–12, 35: 2) it is similar to the next subspecies, differing in the irregular shape of elongate cornuti patch M1-M2-M3-M4-B of right side of vesica; cornuti patch O is large.

C. t. vacillans (Walker, 1855); List Specimens lepid. Insects Colln. Br. Mus. **3**: 685 (*Amphissa vacillans*); type locality: "Hong Kong" (Fig. 4).

=*Creatonotos transiens orientalis* Nakamura, 1976, **syn. nov.**, Tyô to Ga **27** (3): 116, fig. 1 (3), 3 (5); type locality: "Fang, Thai" [Thailand].

China: Heilongjiang (Tili, Pingdin Mt., SZMN; according to the general species distribution, this outlying northern locality needs confirmation), Shanxi, Shaanxi, Shandong, Anhui, Henan, Jiangsu, Zhejiang, Fujiang, Jiangxi, Hubei, Hunan, Guangdong, Hainan, Guanxi, Guizhou, Sichuan, Yunnan (FANG 2000), East and South Tibet (FANG

1982, 1987); Indochina, Peninsular Malaysia, Sumatra, Borneo.

Remarks. This subspecies is paler than the nominotypical one (taking into account specimens from Sikkim), cornuti patch M1-M2-M3-M4-B on the vesica right side is not massive, equal in width, but varies in length, cornuti patch O is also large (Figs 16–21, 35: 5). The original description of *vacillans* was based on a single (therefore holotype) male. However, WALKER (1856: 1702) later described *Aloa vacillans*, referring to three specimens: a "typical" female from N. India; var. beta, a male of *wilemani* from the Philippines; var. gamma, the holotype Hong Kong male of the original *vacillans*. This may be a further indication that Walker did on occasion "recycle" his type material!

C. t. sundana Nakamura, 1976, Tyô to Ga **27** (3): 116, fig. 1 (2), 3 (4); type locality: "Mégamenden, Java" (Fig. 5).

Indonesia: Siberut (Bojakan, SZMN), Java, Bali (Tamblingan, SZMN), east to Lombok.

Remark. This island subspecies does not differ from the typical subspecies in wing colouration, but it has reduced cornuti patches M1-M2-M3-M4-B and O on vesica (Figs 22–24, 35: 4).

C. t. koni Miyake, 1909, **stat. rev.**; Bull. Coll. Agric. Univ. Tokyo **8** (2): 169 (*Creatonotus Koni*); type locality: "Mt. Arisan in Formosa" (Fig. 6).

Taiwan, Japan: Yonagumi, Iriomote, Ishigaki, Miyako, Okinawa, Okinoerabu, Amami, Yaku (NAKAMURA 1976; INOUE 1982).

Remarks. According to NAKAMURA (1976) this subspecies is characterized by the very light rosy tone of head, patagia, tegulae, thorax and forewings; cornuti patch M1-M2-M3-M4 is divided into separate small cornuti groups, while cornuti patch O is not reduced (Figs 25–27, 35: 3).

Creatonotos wilemani (Rothschild, 1933)

Ann. & Mag. Nat Hist. (10) **11**: 183–184 (*Creatonotus wilemani*); type locality: "Palali, 2000 ft., Benguet, Klondyke, 800 ft., Benguet, Luzon, …, Kolambugan, Lanao Plains, Mindanao, …; Luzon…" (Fig. 7).

=*Creatonotos philippinensis* Nakamura, 1976, Tyo to Ga **27** (3): 113–114, fig. 1 (4), 3 (6); type locality: "Subasta, Mindanao Is."

Philippines: from Luzon to Mindanao.

Remarks. The species is characterized by absence of black dots at forewing discocellular veins, presence of the largest peniculi or finger-like processes at base of the transtilla, which is wide and the most strongly sclerotized in the whole group (Figs 28–30, 35: 6).

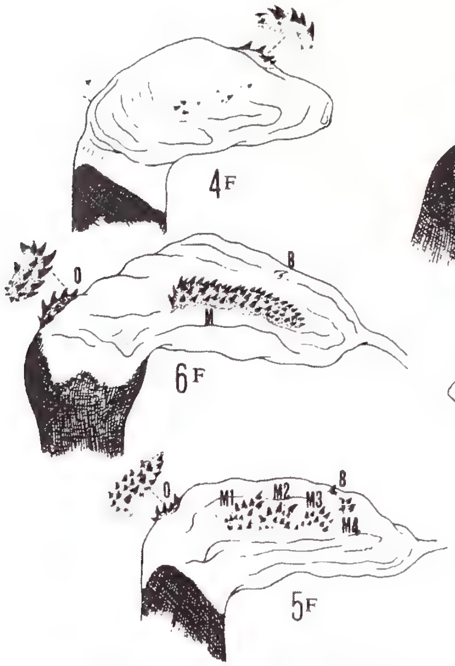
Creatonotos kishidai Dubatolov & Holloway, sp. nov. (Figs 8–9)

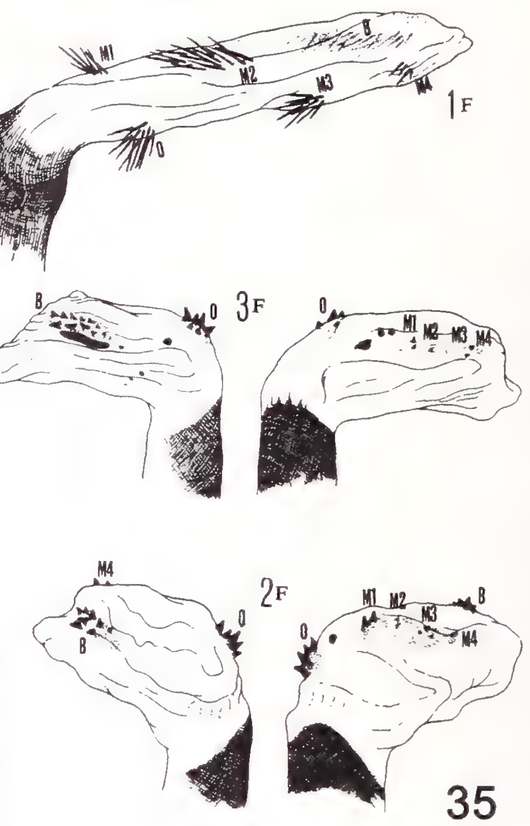
Material. Holotype – male, Indonesia, Sulawesi, Tondano, VII 1988, native collector leg., received from Y. Kishida. Preserved in SZMN coll. (http://szmn.sbras.ru). Paratypes: 1 ♂, the same data (SZMN); 2 ♂ (BMNH genitalia slides 2313, 2314), 1 ♀ (BMNH slide 2311), Koelawi, Paloe [Palu], 3100', W. Celebes, March 1937, J. P. A. Kalis (BMNH); 1 ♂ (BMNH slide 2312), Loda, Paloe [Palu], W. Celebes, 4000', May 1937, J. P. A. Kalis (BMNH); 3 ♂, the same data (Zoologisches Forschungsinsmuseum Alexander Koenig, Bonn, Germany); 1 ♀ (syntype of *transiens*), Celebes [Menado], [Madame Ida] Pfeifer coll. (BMNH). There are large numbers of specimens of *C. kishidai* in BMNH from the localities listed for the paratypes, but we have restricted these to dissected specimens and to the syntype of *transiens*.

Description. Male forewing length 21.0–22.5 mm, wing expanse 41.0–46 mm. Wings dark grey, the forewing with lighter costal margin and veins on the external part of the wing. There are three or four black dots around the discocellular veins, two inside the cell being larger. Head and thorax whitish, abdomen dorsally yellow with one dorsal and two lateral rows of black spots; ventrally it is grey.

Male genitalia (Figs 31–34). Uncus elongate, horn-like. Valvae narrow, elongate, slightly curved inwards, with two distal processes: the apex and a lateral spur. Juxta longer than wide, its apical lateral sides covered with small spines. Transtilla at both bases with distinct finger-like processes (peniculi). Aedeagus straight, widened at apex, where it is enveloped by a sclerotized spine-bearing band (hypertrophied cornuti patch O); this band is sometimes disrupted ventrally (Fig. 34). Vesica with two elongate sclerotized cornuti patches M and B, between them there is one more small round sclerotization B on the opposite side of the vesica.

Female forewing. Length 22.0–23.0 mm, wing expanse 43.0–49.0 mm, the syntype of *transiens* being at the upper boundary of this range. Forewings light grey with lighter veins in external part of the wing. There are four black dots around the discocellular veins, two inside the cell being larger; the external anterior one is the weakest. Hindwings whitish with dark scales on veins; those on the cubital stem are darkest.





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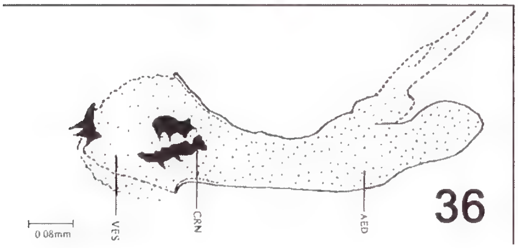

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Figs 35–36. 35. Vesica structure of the *Creatonotos* species, by Nakamura (1976). 1. *C. gangis*, 2. *C. t. transiens*, 3. *C. t. koni*, 4. *C. t. sundana*, 5. *C. t. orientalis* (= *vacillans*), 6. *C. t. philippinense* (= *wilemani*). O, M1, M2, M3, M4, B – cornuti patches. **36.** Aedeagus structure (vesica only slightly everted) of *C. ananthakrishanani*, from original description by KIRTI & KALEKA (1999). AED – aedeagus, CRN – cornuti, VES – vesica.

Remarks. The presence of a sclerotized spine-bearing band, which envelops the aedeagus apex, distinguishes the new species from both *C. transiens* and *C. wilemani*, where it is absent. Moreover, these two species lack the spining of the juxta characteristic of the new species. The presence of small peniculi (finger-like processes) at the bases of the transtilla is shared with *C. wilemani* (Figs 28, 31), though this species has them larger on a larger and more sclerotized transtilla. The valves also differ across the three species, extending beyond the uncus in *C. transiens*, but falling short of it in *C. kishidai* and *C. wilemani*; the lateral spur is short and in the most basal position in *C. transiens*, but nearer the apex of the valve and longer in *C. kishidai*, where distinct bilateral asymmetry occurs, the right valve being longer, with the apical process longer beyond the lateral spur. In *C. wilemani* the lateral spur is small and very close to the apex.

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Herpetofauna Kakamegensis – The amphibians and reptiles of Kakamega Forest, western Kenya

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Abstract. We present an annotated checklist of the herpetofauna of Kakamega Forest with comments on the biology and systematics of the taxa. Twenty-five amphibian, one turtle, 22 lizard and 36 snake species are recorded from within the forest and its immediate environment. We discuss the generalized zoogeography of the forest and distribution pattern of the taxa comment on the protection of the forest. Analysis of the reptile species composition shows Kakamega Forest to be similar to the Guinea-Congolian rainforest and is considered the easternmost remnant of this forest block. Kakamega forest has a high diversity value for Kenya and represents a diversity hotspot on a national scale. Two species, *Lygodactylus gutturalis* and *Psammophis phillipsi*, are recorded in Kenya for the first time. Several other first records and the description of a new species (Agamidae: *Agama finchi*) were published already separately.

Keywords. East Africa, Kenya, Kakamega Forest, herpetological survey, checklist, national diversity hotspot.

1. INTRODUCTION

In Africa tropical rainforests extend from southern Senegal in the west to the coastal forests of Kenya and Tanzania in the east (COLLINS 1992). The East African rainforests belong to different biogeographical clades. Apart from the mountain forests and inselbergs, which are not clearly assignable, there are three important forest types: the coastal forests and the Eastern Arc mountain forests, both with a high degree of endemism, and the easternmost outliers of the Guinea-Congolian rain forest. The Eastern Arc Mountains were already the object of several biological studies and have recently been reviewed in respect to their herpetofauna by HOWELL (1993). The value of the coastal forest biodiversity was underestimated for a long time. Recently the herpetofauna of the Kenyan part of the coastal forest was surveyed by the Kifcon project (KIFCON 1995). Only the forests associated with the Guinea-Congolian forest (e. g. Budongo, Bwamba, Kibale, Bwindi, Mbira and Mt. Elgon in Uganda) are at least partly explored. Herpetological inventories have been made for the Bwindi (DREWES & VINDUM 1991) and Kibale Forests (VONESH 2001). All together these forests harbour an estimated number of 333 amphibian (DUELLMAN 1993), 105 snake (HUGHES 1983), 95 lizard, 16 turtle and 3 crocodilian species (BAUER 1993). This total herpetofaunal species richness is more than 550. Considering the fact that zoological research in Africa is becoming more and more difficult because of the political instabilities in numerous countries, this number is certainly too low. Because tropical forests in Africa are seriously threatened numerous undescribed species may become extinct before their discovery and scientific descriptions. Uganda, for example has lost 86 % of its original forest in the past two decades and the remaining parts are isolated fragments (VONESH 2001).

Kakamega Forest in western Kenya is a similar isolated fragment. This small forest is the easternmost fragment of the equatorial rain forest system (CLAUSNITZER 2005; DREWES 1976; HAMILTON 1976; KÖHLER 2004; KOKWARO 1988; SCHIØTZ 1976; VONESH 2001; WAGNER et al. submitted; ZIMMERMANN 1972) and has recently been surveyed in regard to its faunal communities by the 'BIOTA East Africa Project' and especially to its amphibian fauna by e. g. SCHICK et al. (2005) and LÖTTERS et al. (2006). The herpetogeographical relationships to other fragments of the equatorial rain forest and other tropical forests have recently been discussed by WAGNER et al. (subm.). Despite belonging to Guinea-Congolian forest, Kakamega Forest contains also numerous Afromontane elements (MUTANGAH et al. 1992; BENNUN & NJOROGE 1999) in its flora and fauna. Therefore, the forest has a very large diversity and zoogeographical value which has been shown by several authors for the different species groups (e. g. Odonata: CLAUSNITZER 1999 & 2005; Amphibia: SCHICK et al. 2005; Reptilia: this paper; Aves: ZIMMERMANN 1972) and a lot of species are not found elsewhere in Kenya. Additionally, most of the remaining closed canopy forest within the country is found in western Kenya (WASS 1995). On a national scale, the forest can be considered as a diversity hotspot and needs efficient protection. On the pan-African

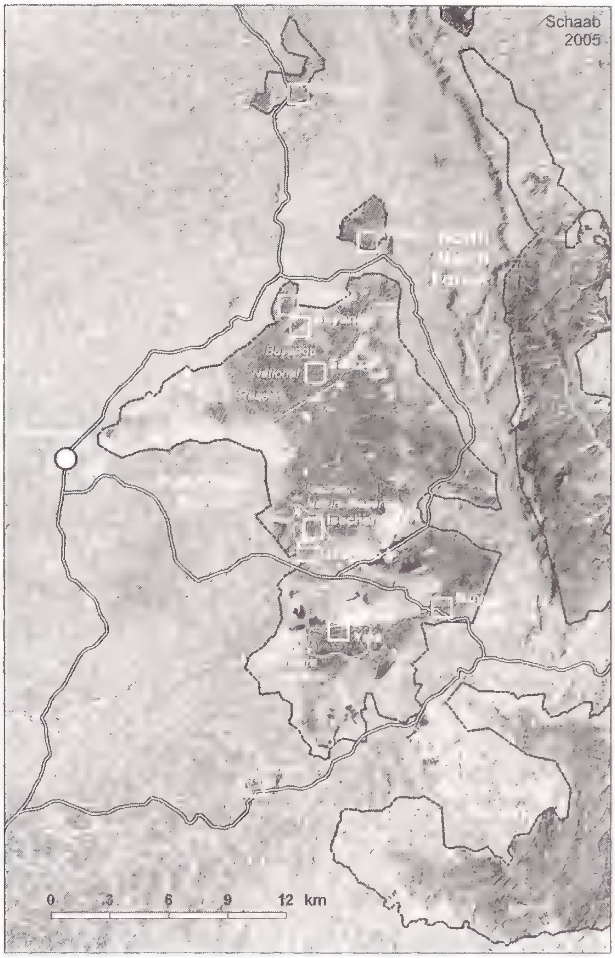

Fig. 1. The main areas of investigation of BIOTA East Africa in the Kakamega Forest in the background a subset of a Landsat 7 (ETM+) scene from 5 Feb 2001, contrast-enhanced band combination 5/4/3 for within-forest differentiation but printed in black and white. (Courtesy to G. SCHAAB of BIOTA – E02).

scale, Kakamega forest is not considered as a hot-spot because in comparison with e. g. the Mt. Nlonako in Cameroon (99 amphibian [HERRMANN et al. 2005a] and 89 reptile species, [HERRMANN et al. 2005b]) the diversity is comparatively low.

Compared with other vertebrate groups, East African amphibians and reptiles are rather poorly studied and insufficiently known. In order to provide conservationists data for defining priorities for conservation it is necessary to obtain basic information on the diversity and community of forest amphibians and reptiles.

Amphibians have been intensively studied by several authors within the 'Biota East Africa Project' (e. g. SCHICK et al. 2005; LÖTTERS et al. 2004; LÖTTERS et al. 2006; KÖHLER et al. 2006) whereas reptiles have been surveyed only superficially in the Kaimosi fragment by LOVERIDGE (1935, 1936) and in the main forest by DREWES (1976). Subsequently no further reports on Kakamega reptiles have been published apart from the mentioning of single voucher specimens as e. g. in SPAWLS et al. (2002) and publications arising from this study (BÖHME et al. 2005; KÖHLER et al. 2004; WAGNER & SCHMITZ 2006; WAGNER et al. subm.).

The aim of the present paper is to provide an overview of the herpetofauna of this forest as basic information for conservationists and wildlife biologists and to highlight the importance of the Kakamega Forest because of its impact and value on the biodiversity of Kenya.

2. DESCRIPTION OF THE STUDY AREA

Kakamega Forest is situated in the Kakamega District near Kakamega town in the Western Province of Kenya. The forest extends from 0°10' and 0°21 N to 34°47' and 34°58'E, covering an area of 240 km^2, of which only 44.55 km^2 are protected by law (MITCHELL 2004).

The forest altitude varies between 1500 and 1700 m a.s.l. (above sea level) averaging 1650 m a.s.l. The forest becomes part of the stratified landscape of the East African Rift Valley, situated 150 km to the east. The annual precipitation ranges from 1500 to 2300 mm. The annual average temperature is 27 °C at daytime and 15 °C at night. Two important rivers traverse the forest: the Isiukhu River in the north and the Yala River in the south. Both have their source in the Nandi Escarpment and drain into the nearby Lake Victoria. The forest block itself is surrounded by several forest fragments (e. g. Kisere, Malaba, Kaimosi), which differ in size, in the degree of destruction and their conservation status. The most important of these are the Kisere in the north and the Kaimosi fragment in the south. Kisere is protected as a National Reserve whereas Kaimosi is unprotected but well known historically from several collections made by A. LOVERIDGE and from the three herpetological taxa described by him from Kaimosi and named after this forest: *Agama kaimosae*, *Typhlops kaimosae* and *Dendroaspis jamesoni kaimosae*.

The eastern border of the forest is the 2200 m high Nandi Escarpment with its Northern Nandi and Southern Nandi forest. Both are considered to be montane forests because of the occurrence of the tree fern *Cyathea manniana* as an indicator species of this forest type. The forests were contiguous with the Kakamega forest system until recently. MITCHELL (2004) pointed out that the North Nandi forest was not connected with Kakamega forest in the 20th century although there was "dense forest" in the 1960´s between South Nandi forest and Kakamega Forest.

Collection sites mentioned in this paper are as follows: the 'Buyangu area' is the name of the northern part of the Kakamega National Reserve ('primary-like' forest), with the Buyangu Village on his northern margin. Salazar Circuit is an old plantation within the National Reserve, which is now secondary forest dominated by guava. Udo´s Campsite is located within the northern part of the National Reserve and is the home of the BIOTA field camp. Isecheno is the low protected southern part of the forest. Rondo Retreat Centre is a small hotel within this area.

3. MATERIAL AND METHODS

The material presented in this paper was partly collected during a three-month herpetological mission by the senior author, which was carried out between March and June 2003. It was completed by some older voucher material from Kakamega Forest in the ZFMK collection, collected by H.W. HERRMANN, D. MODRY and P. NECAS. Material from Kakamega Forest is also part of the collections of CAS, MHNG, NHMW, NMK, USNM, but this material was only partly analysed by the authors. Relevant literature data was also evaluated. During the 2003 mission 170 reptiles were collected. Amphibians were not the main emphasis of the study but also collected and compared with the species list presented by SCHICK et al. (2005). Specimens of the study were fixed in 98 % ethanol and subsequently transferred to 70 % ethanol. For final deposition, they were equally partitioned between the NMK and ZFMK collections. The main forest and the forest fragments were walked during both day and night and specimens, mostly arboreal, were caught dominantly by visual encounter surveys along transects and opportunistic searches. In addition, Y-shaped drift-fences with pitfalls were used for terrestrial species. Catching success was low; only *Adolfus africanus* (Lacertidae) and amphibians were caught using this method. The roads were patrolled for snakes and the human inhabitants of the surrounding villages were recruited to help with collecting.

The individual species accounts include the following parts: *Specimens examined*: gives a list of the material from museums collections examined by the authors; *Additional specimens*: refer to material known from other collections and not examined by the authors; *Key references*: lists publications with more detailed information on species of Kakamega forest; *Remarks*: gives information about the collected specimens and taxonomic statements.

We follow mostly the classification and taxonomic conclusions of FROST et al. (2006), however there are several taxonomic conclusions in their amphibian tree of live tat we can not fathom and in our opinion require additional evidence and study.

Collection codens: BIOTA= Biomonitoring Transect Analysis in Africa; BMNH = The Natural History Museum (British Museum [Natural History]), London, England; CAS= California Academy of Science, San Francisco, USA; MCZ= Museum of comparative Zoology, Harvard University, Cambridge/Massachusetts, USA; MHNG= Muséum d´histoire naturelle, Geneva, Switzerland; NHMW= Naturhistorisches Museum Wien, Vienna, Austria; NMK= National Museums of Kenya, Nairobi, Kenya; PW= field number of the senior author; USNM= National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; ZFMK= Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

4. RESULTS

4.1. Checklist of the herpetofauna of Kakamega Forest

Amphibia

Pipidae Gray, 1825

Xenopus victorianus Ahl, 1924

1924 *Xenopus victorianus* Ahl, Mitt. Zool. Mus. Berlin, 11: 270.

Specimens examined. ZFMK 81733-735, 81940.

Additional specimens. NMK A/3874/1, A/3935, A/3944, A/4025/1-2, A/4062/1-8, A/4163.

Key references: SCHICK et al. 2005.

Remarks: This species was often found in drift fence buckets in the Buyangu area near a small pond within the forest (ZFMK 81940). It was also found at Rondo Retreat in the southern part of the forest (ZFMK 81735). The vouchers are assigned to *Xenopus victorianus* in SCHICK et al. (2005) and to *Xenopus* sp. in LÖTTERS et al. (2006).

Bufonidae Gray, 1825

Amietophrynus kisoloensis (Loveridge, 1932)

1932 *Bufo regularis kisoloensis* Loveridge, Occas. Pap. Boston Soc. Nat. Hist., 8: 52.

Specimens examined. ZFMK 81727-730, 81943.

Additional specimens. NMK A/104-106, A/108, A/1072/1-2, A/1293/1-2, A/1318/1-2, A/1648/1-3, A/2046/1-4, A/3055/1-3, A/3104/1-3, A/3153/1-9, A/3563/1-2, A/3750/1-3, A/3813, A/3850/2, A/3851/1-3, A/3943.

Remarks: ZFMK 81727-728 were collected in the Buyangu area. ZFMK 81943 was found in the Malaba fragment of the forest. ZFMK 81729 and A/3055/1-3 are from Rondo Retreat Centre, NMK A/3104/1-3 from Isecheno forest camp both located in the southern part of the forest. NMK A/3850/2 was collected at the Isiukhu falls in the Buyangu area.

Amietophrynus maculatus (Hallowell, 1854)

1854 *Bufo maculatus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 7: 101.

Specimens examined. ZFMK 77458, 81723-726, 81941-942.

Additional specimens. NMK A/1194, A/3850/1,3-10.

Remarks: ZFMK 81941-942 were collected within Buyangu Village along a road under stones next to a stream. NMK A/3850/5 was collected at the Isiukhu falls in the Buyangu area. NMK A/1194 was from the Malava forest fragment.

Ranidae Rafinesque, 1814

Hoplobatrachus occipitalis (Günther, 1859)

1859 *Rana occipitalis* Günther, Arch. Naturgesch., 24: 320.

Specimens examined. NMK A/3938.

Key references: SCHICK et al. 2005.

Remarks: The voucher was collected in a swamp in the Buyangu area. Specimens, both adults and tadpoles, were found in an old swimming pool of the Serena Island Lodge in Kakamega town and were documented by a voucher specimen (NMK uncatalogued) and photographs.

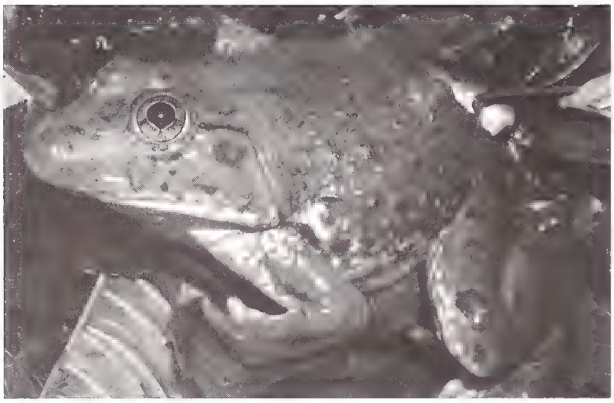

Fig. 2. *Hoplobatrachus occipitalis* from Kakamega town. Photo by Jörn KÖHLER.

Phrynobatrachus graueri (Nieden, 1911)

1911 *Arthroleptis graueri* Nieden, Sitzungsber. Ges. Naturforsch. Freunde Berlin, 1910: 441.

Specimens examined. None.

Additional specimens. NMK A/198, A/3105/2.

Key references: LÖTTERS et al. 2006.

Remarks: The specimen NMK A/198 was collected on a bridge near Kakamega town. NMK A/3105/2 was collected at the Kalunga glade at the Kakamega Forest.

Phrynobatrachus aff. *mababiensis* FitzSimons, 1932

1932 *Phrynobatrachus mababiensis* FitzSimons, Ann. Transvaal Mus., 15: 40.

Specimens examined. None.

Remarks: This species has only been recorded from literature (SCHICK et al. 2005) and is currently under investigation by SCHICK et al. (2005) and other colleagues.

Phrynobatrachus natalensis (Smith, 1849)

1849 *Stenorhynchus natalensis* Smith, Ill. Zool. S. Afr., 3 (Appendix): 24.

Specimens examined. ZFMK 81742-43.

Additional specimens. NMK A/3105/1, A/3863/1-4, A/3931, A/3932.

Remarks: NMK A/3105/1 was from the Kalunga glade within the Kakamega forest area. The series NMK A/3863 and the ZFMK vouchers were from the Buyangu area. Details on the other vouchers are unknown.

Phrynobatrachus aff. *minutus* (Boulenger, 1895)

1895 *Arthroleptis minutus* Boulenger, Proc. Zool. Soc. London, 1895: 539.

Specimens examined. None

Additional specimens. NMK A/3924/1-6, A/4310.

Key references: LÖTTERS et al. 2006.

Remarks: Details on the vouchers are unknown. NMK A/3924/1,2,5 are on permanent loan to the ZFMK. This taxon was not recorded by SCHICK et al. (2005).

Afrana angolensis (Bocage, 1866)

1866 *Rana angolensis* Bocage, J. Sci. Math. Phys. Nat., Lisboa, 1: 73.

Specimens examined. NMK A/100/1-8, A/101, A/102/1-2.

Additional specimens. NMK A/1294/1, A/1314/1-8, A/1649/1-3, A/3639, A/3937/1-2, A/4239.

Key references: LÖTTERS et al. 2006.

Remarks: NMK A/4239 was found along the Salazar road. The series NMK A/1314/1-8 and A/1649 were collected at the Ikuywa River. Details on the other specimens are unknown.

Amnirana cf. *albolabris* (Hallowell, 1856)

1856 *Hyla albolabris* Hallowell, Proc. Acad. Nat. Sci. Philadelphia, 8: 153.

Specimens examined. None.

Additional specimens. NMK A/196/1-2, A/1966.

Key references: Schick et al. 2005; Lötters et al. 2006.

Remarks: The specimens NMK A/196/1-2 came from Kakamega town, near the Forest Department Pump House.

Ptychadena anchietae (Bocage, 1867)

1867 *Rana anchietae* Bocage, Proc. Zool. Soc. London, 1867: 843.

Specimens examined. NMK A/3845.

Additional specimens. A/4212, A/4216, A/4220/1-2, A/4224, A/4226/1-2, A/4234/1-3.

Remarks: NMK A/4212 was collected in a small puddle near the Buyangu view point; NMK A/4220/1-2 were collected in amplexus on the 28.IV.2004 from the same puddle. NMK A/4216 was found in short grass habitat next to a small puddle within the Salazar secondary forest. NMK A/4224 was collected on new Buyangu Campsite. NMK A/4234/1 was collected near the Keep office, A/4234/2-3 near the Isecheno Primary school. Details on the other specimens are unknown.

Ptychadena porosissima (Steindachner, 1867)

1867 *Rana porosissima* Steindachner, Reise Österreichischen Fregatte Novara, Zool.: 18.

Specimens examined. None.

Additional specimens. NMK A/3107/1-3, A/3574, A/4222.

Key references: Schick et al. 2005; Lötters et al. 2006.

Remarks: NMK A/3107/1-3 were collected at Kalunga glade. NMK A/4222 was found calling on wet mud near a water edge in the Buyangu area. Details of the other specimen are unknown.

Ptychadena taenioscelis Laurent, 1954

1954 *Ptychadena taenioscelis* Laurent, Ann. Mus. R. Congo Belge, Tervuren, Zool., 34: 25.

Specimens examined. None.

Additional specimens. NMK A/3955/1-2, A/4213.

Key references: Lötters et al. 2006.

Remarks: NMK A/4213 was found in a small swamp at the Buyangu area. Details on the other voucher are unknown. This species was recorded for the first time for Kenya by Lötters et al. (2006) and at present is only known to occur in Kakamega Forest within Kenya.

Ptychadena aff. *mascareniensis* (Duméril & Bibron, 1841)

1841 *Rana mascariensis* Duméril & Bibron, Erp. Gen., 8: 350.

Specimens examined. ZFMK 81944.

Additional specimens. NMK A/3572, A/3840/4-5, A/3856, A/4214, A/4217/1-2, A/4221, A/4223, A/4227/1-10, A/4229/1-2, A/4232/1-4, A/4235/1-9.

Key references: Vences et al. 2004; Lötters et al. 2006.

Remarks: *P. mascareniensis* was often found on the shore of the Isiukhu River in its small discharging streams and in the Buyangu area. NMK A/4227/1-3 was found near the Keep Office at Isecheno, NMK A/4227/4-10 in a temporary swamp at Isecheno. This taxon was listed by Lötters et al. (2006) as *Ptychadena* aff. *mascareniensis*.

Ptychadena oxyrhynchus (Smith, 1849)

1849 *Rana oxyrhynchus* Smith, Ill. Zool. S. Afr., 3(Part 28): pl. 77, fig 2.

Specimens examined. None.

Additional specimens. NMK A/103/1-2, A/3846, A/4211, A/4215/1-4, A/4218, A/4219/1-3, A/4225/1-2, A/4228/1-3, A/4230/1-2, A/4231/1-2, A/4233/1-4, A/4236/1-2.

Key references: Lötters et al. 2006.

Remarks: NMK A/4225/1-2, A/4228/1-3 and A/4236/1-2 were collected in a pond on the new Buyangu Campsite, NMK A/4231/1-2 was found there in amplexus on the 31. V. 2004 and the female laid eggs over night. NMK A/4233/1-4 were found at Isecheno in the southern part of the forest. Details on the other specimens are unknown. This taxon was listed by Lötters et al. (2006) as *Ptychadena* aff. *oxyrhynchus*.

Hyperoliidae Laurent, 1943

Afrixalus osorioi (Ferreira, 1906)

1906 *Rappia osorioi* Ferreira, J. Sci. Math. Phys. Nat., Lisboa, Ser. 2, 7: 162.

Specimens examined. NMK A/3927/2.

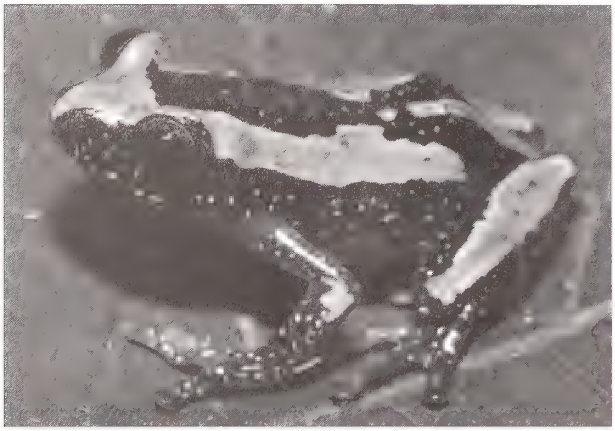

Fig. 3. *Afrixalus osorioi* from Kakamega Forest. Photo by Jörn KÖHLER.

Additional specimens. A/3928, A/4017, A/4316/1-7.

Key references: KÖHLER et al. 2005.

Remarks: NMK A/3927/2 is on permanent loan to the ZFMK. NMK A/4017 and the series A/4316 were collected at a pond within the Buyangu area. One specimen was additionally sighted in the South Nandi forest. This species was recorded for the first time for Kenya by KÖHLER et al. (2005) and at present only occurs in the Kakamega Forest complex within Kenya.

Afrixalus quadrivittatus (Werger, 1908)

1908 '1907' *Megalixalus leptosomus leptosomus* Werger, Sitzungsber. Akad. Wiss. Wien, Phys. Math. Naturwiss. Kl., 116: 1900.

Specimens examined. NMK A/3933/2.

Additional specimens. NMK A/3933/1, A/4317/1-7.

Key references: KÖHLER et al. 2005.

Remarks: NMK A/3933/2 is on permanent loan to the ZFMK and was collected at a swamp in the Buyangu area. The series NMK A/4317 was collected at the pond of the Buyangu area.

Hyperolius acuticeps Ahl, 1931

1931 *Hyperolius acuticeps* Ahl, Das Tierreich, 55: 282.

Specimens examined. ZFMK 77616, 81749-750.

Additional specimens. NMK A/3922/2.

Key references: LÖTTERS et al. 2006.

Remarks: ZFMK 81749-750 were from the Buyangu area. Details on the other vouchers are unknown.

Hyperolius kivuensis Ahl, 1931

1931 *Hyperolius kivuensis* Ahl, Das Tierreich, 55: 280.

Specimens examined. ZFMK 81745-746, 82183-184.

Additional specimens. NMK A/3032/1-16, A/3103, A/3579, A/3709, A/3710, A/3748/1-4, A/3825/1-6, A/3864/4, A/3867/1-5, A/3953, A/4011/1-2, A/4026/1-2, A/4065.

Key references: SCHICK et al. 2005; LÖTTERS et al. 2006.

Remarks: NMK A/3103, A/3867, A/4011, A/4026 and ZFMK 81745-746 were from the Buyangu area. NMK A/4065 was collected at the BIOTA Campsite. Details on the other vouchers are unknown.

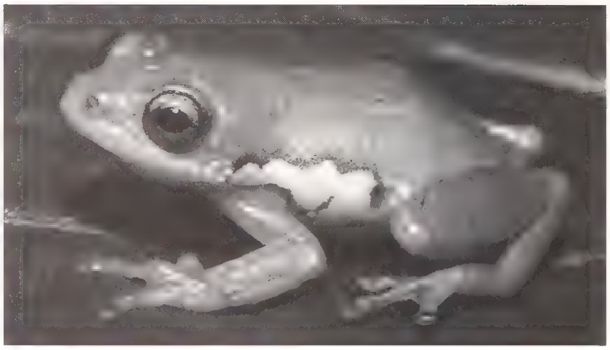

Fig. 4. *Hyperolius lateralis* from Kakamega Forest. Photo by Jörn KÖHLER.

Hyperolius lateralis Laurent, 1940

1940 *Hyperolius lateralis* Laurent, Rev. Zool. Bot. Afr., 34: 1.

Specimens examined. ZFMK 81747-748.

Additional specimens. NMK A/2075/5-6, A/2075/8-10, A/3925/1-4, A/3936.

Remarks: NMK A/3925/1 is on permanent loan to ZFMK. ZFMK 81747-748 were from the Buyangu area. NMK A/3936 was from Rondo Retreat Centre in the southern part of the forest. Details on the remaining vouchers are unknown. Within Kenya, this taxon is currently only recorded from the Kakamega Forest.

Hyperolius viridiflavus (Duméril & Bibron, 1841)

1841 *Eucnemis viridi-flavus* Duméril & Bibron, Erp. Gen., 8: 528.

Specimens examined. ZFMK 77426, 81950.

Additional specimens. NMK A/3056/1-3, A/3578, A/3866/5-11, A/668/1-4, A/1193/1-2, A/1444/1-5, A/3749, A/3809/1-5, A/3954/1-2, A/4013, A/4027/1-3, A/4066.

Remarks: Details on the vouchers are unknown, but most are from the Buyangu area. *H. viridiflavus* is the most common frog inside the forest. Specimens were observed at different ponds and also clearings for example, the BIOTA field camp, where several specimens were sitting inside the lavatory. NMK A/1193/1-2 were from Malava forest.

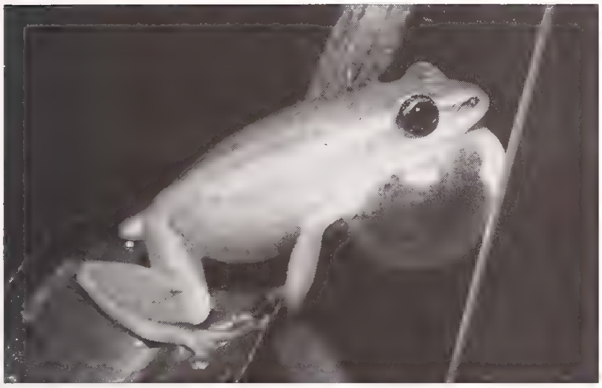

Fig. 5. *Hyperolius cinnamomeoventris* from Kakamega Forest. Photo by Jörn KÖHLER.

Hyperolius cinnamomeoventris Bocage, 1866

1866 *Hyperolius cinnamomeo-ventris* Bocage, J. Sci. Math. Phys. Nat., Lisboa, 1: 75.

Specimens examined. ZFMK 77431-432, 81744.

Additional specimens. NMK A/2095/1, A/3858/1-2, A/3918/1-2, A/4012.

Key references: SCHICK et al. 2005; LÖTTERS et al. 2006.

Remarks: NMK A/3858, A/4012 and ZFMK 81744 are from the Buyangu area. This taxon was reported by LÖTTERS et al. (2006) as *Hyperolius* aff. *cinnamomeoventris*.

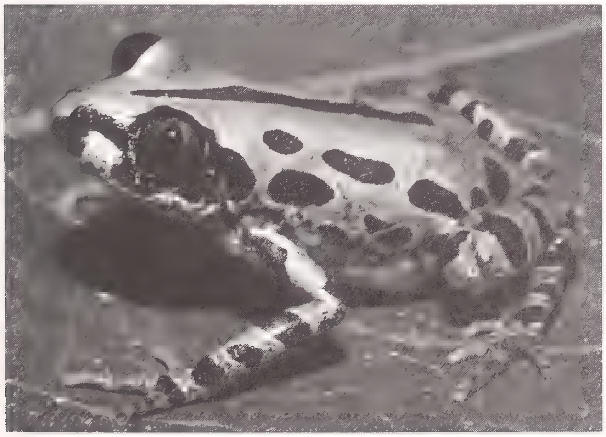

Fig. 6. *Kassina senegalensis* from Kakamega Forest. Photo by Jörn KÖHLER.

Kassina senegalensis (Duméril & Bibron, 1841)

1841 *Cystignathus senegalensis* Duméril & Bibron Erp. Gen., 8: 418.

Specimens examined. ZFMK 81741, 81946-949.

Additional specimens. NMK A/1158, A/1317, A/3711, A/3920.

Remarks: All vouchers were from the Buyangu area and some were collected with a drift fence next to a pond. One specimen was collected on the Buyangu Hill outside the forest under stones.

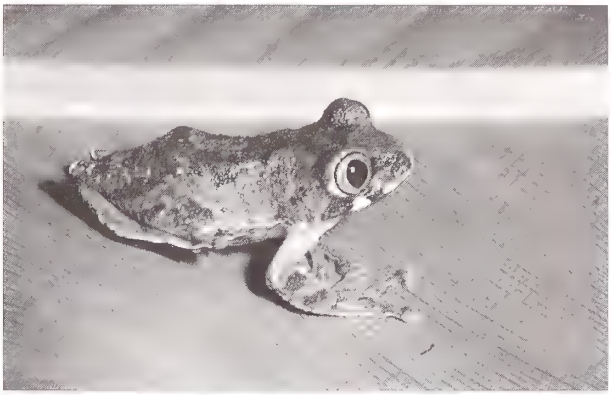

Fig. 7. *Leptopelis mackayi* from Kakamega Forest. Photo by Arne SCHIØTZ.

Arthroleptidae Mivart, 1869

Leptopelis mackayi Köhler, Bwong, Schick, Veith & Lötters, 2006

2006 *Leptopelis mackayi* Köhler, Bwong, Schick, Veith & Lötters, Herpetological Journal 16: 183-189.

Specimens examined. ZFMK 83304-305 (paratypes), ZFMK 83306.

Additional specimens. NMK A/3057/1 (holotype), NMK A/1407/1-3 (paratypes), NMK A/3072/1.

Key references: KÖHLER et al. 2006.

Remarks: This species was recently described by KÖHLER et al. (2006) and is only known from Kakamega Forest and its vicinity and inhabits so far only forest habitats (also secondary and disturbed forest). It represents the sister taxon of the West African *L. modestus* and was referred to this species in the past by SCHIØTZ (1975, 1999).

Leptopelis aff. *bocagii* (Günther, 1865)

1865 "1864" *Cystignathus bocagii* Günther, Proc. Zool. Soc. London, 1864: 481.

Specimens examined. None.

Additional specimens. UZM R/074960-2.

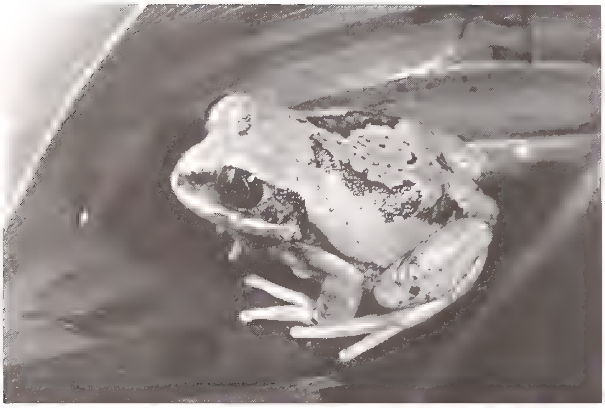

Fig. 8. *Leptopelis* aff. *bocagii* undescribed form from Kakamega Forest. Photo by Arne Schiøtz.

Key references: Schiøtz 1975.

Remarks: Schiøtz (1975) collected two males and one female (UZM R/074960-2). These vouchers were taken from a savannah-like clearing near the Forest Station in Kakamega Forest. One male was sitting in the bush when calling. See Schiøtz (1975) for more details on the call. *L.* aff. *bocagii* is an undescribed species, very close in morphology to *L. bocagii*. Only a few specimens are known, all from Kakamega (A. Schiøtz, pers. comm.).

Reptilia

Agamidae Spix, 1825

Acanthocercus atricollis (Smith, 1849)

1849 *Agama atricollis* Smith, llustrations of the Zoology of South Africa. 3 (Reptiles).

Specimens examined. NMK L/2655, 2660/2-3; ZFMK 81952-963.

Additional specimens. CAS 122731-122739.

Key references: Klausewitz 1957.

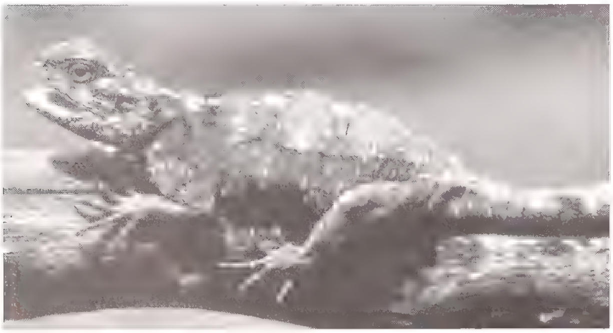

Fig. 9. *Acanthocercus atricollis* from Kakamega Forest. Photo by Philipp Wagner.

Remarks: The debate of the taxonomic status of this species is still ongoing. Many authors (e. g. Boulenger 1896, Klausewitz 1957, Loveridge 1957) have discussed differences or similarities between this taxon and *Acanthocercus cyanogaster* Rüppell 1835. Spawls et al. (2002), Largen & Spawls (2006) and our own morphology studies of the two species support Klausewitz (1957) who regarded them as two distinct species. The reported distribution of both taxa is unclear because of the mentioned taxonomic problems.

Despite the works of Klausewitz (1954, 1957), a new review of the *Acanthocercus*- species complex is needed. The review will be a part of the PhD thesis of the senior author.

The diagnoses of the subspecies of *A. atricollis* by Klausewitz (1957) are not adequate. Therefore, the material is only preliminarily assigned to the subspecies *ugandaensis* because Kakamega Forest is geographically closer to the area of this subspecies than to *minuta*, according to Klausewitz's (1957) map: *A. a. minuta* inhabits Ethiopia and eastern Kenya, while *A. atricollis ugandaensis* occurs within Uganda and western Kenya.

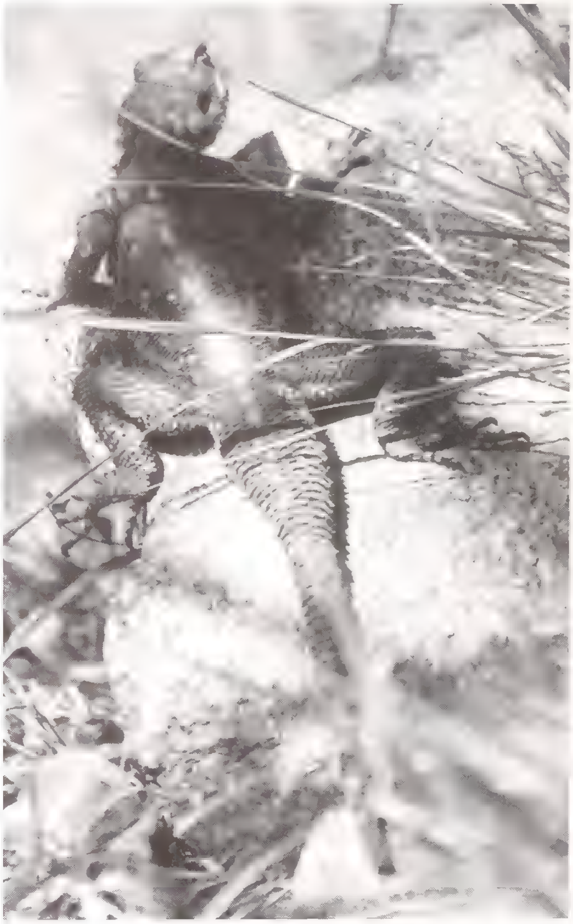

Fig. 10. *Agama kaimosae* from Ngoromosi/ Nandi escarpment. Photo by Alexander Burmann.

This agama subspecies was found in all areas surrounding Kakamega Forest. It reaches the highest density in small villages and Ranger Stations and lives there on the clay huts, in syntopy with *Trachylepis striata* and *Adolfus jacksoni*. It also occurs in hedges close to trees. It was not found inside the forest and also not in plantations and on forest edges.

Agama kaimosae Loveridge, 1935

1935 *Agama agama kaimosae* Loveridge, Bull. Mus. Comp. zool., Harvard 79:10.

Specimens examined. ZFMK 83658-660; NMK L/2715/1,3,4; MCZ 40136- 40150.

Key references: Burmann 2006, Wagner et al. 2007.

Remarks: After its synonymisation by Loveridge (1936), this taxon was regarded as a synonym of *Agama caudospinosa*. But further investigations (Burmann 2006, Wagner et al. 2007) have shown that *Agama kaimosae* is a valid species. The taxon is a SW Kenyan/N Tanzanian endemic (see map in Wagner et al. 2007). The type locality is a rocky highland three miles west of the Friends´ Africa Mission Station at Kaimosi. However no specimens were found there, neither by the senior author in 2003 nor by A. Burmann in 2005. Our specimens were collected in Ngoromosi in the Nandi escarpment.

Chamaeleonidae Gray, 1825

Chamaeleo gracilis Hallowell, 1842

1842 *Chamaeleo gracilis* Hallowell, J. Acad. Nat. Sci. Philadelphia 8: 324.

Specimens examined. NMK L/2203/1, NMK L/2653/1-2; ZFMK 82055-056.

Remarks: The species was not found in Kakamega Forest directly but in forest edge areas of the South Nandi Forest, located slightly east of Kakamega Forest. These forests were united with Kakamega until recently (Mitchell 2004), but in contrast to Kakamega the Nandi Escarpment has montane vegetation. The specimens were found in bushes next to the forest, on the western slopes of the Nandi escarpment.

Chamaeleo hoehnelii Steindachner, 1891

1891 *Chamael(e)o höhnelii* Steindachner, Anz. Akad. Wiss. Wien 28: 141.

Specimens examined. NMK L/252.

Remarks: This voucher was collected in Kakamega town, so it is possible that the species also occurs in the surrounding area of Kakamega Forest.

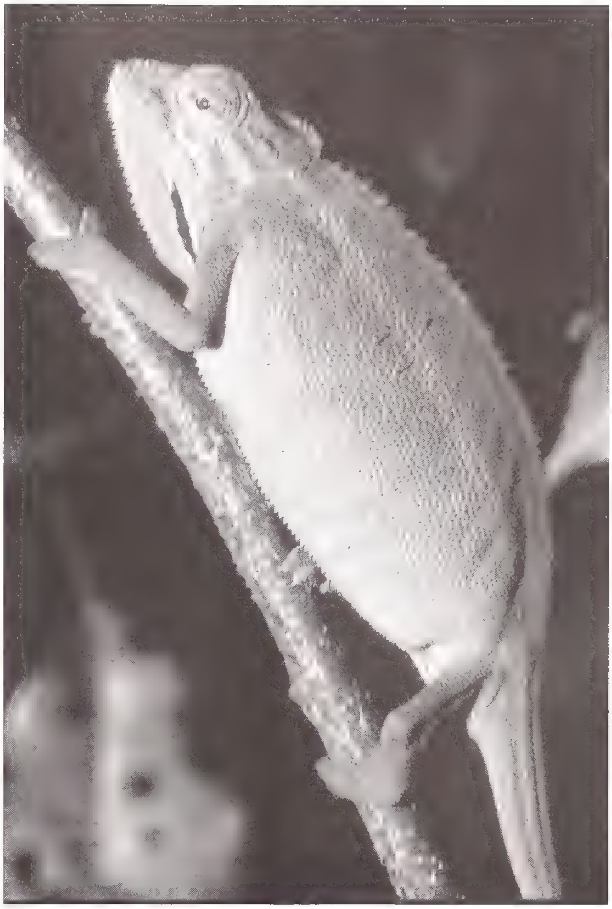

Fig. 11. *Chamaeleo ellioti* from Kakamega Forest. Photo by Philipp Wagner.

Chamaeleo laevigatus Gray, 1863

1863 *Chamaeleo laevigatus* Gray, Proc. Zool. Soc. London 1863: 95.

Specimens examined. NMK L/1588.

Remarks: The only specimen of this taxon was found 1981 by Madsen six kilometres north of Kakamega town. Further data was not available.

Chamaeleo ellioti Günther, 1895

1895 *Chamaeleo ellioti* Günther, Ann. Mag. Nat. Hist., London 15: 524, pl. 21, fig. A.

Specimens examined. NMK L/2480, L/1227, L/1273, L/2647, L/2653/1-2, L/2652/1-2, L/2658; ZFMK 54025, 68494-97, 70835, 81974-80, 82057-58.

Additional specimens. CAS 147912, 153247.

Remarks: The species has a wide distribution in the Kakamega area and specimens were found in several habitats in and around the forest. In the year of the fieldwork

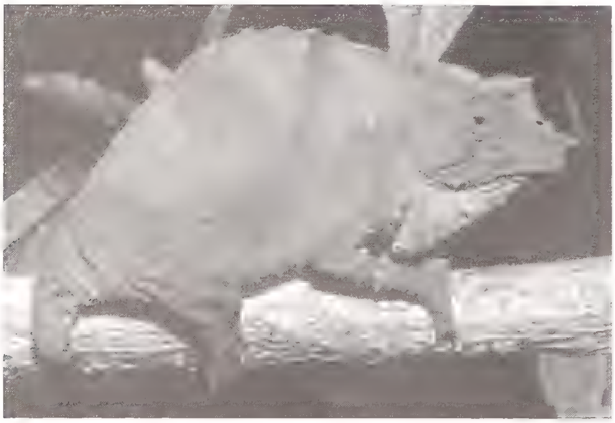

Fig. 12. *Rhampholeon boulengeri* from Kakamega Forest. Photo by Philipp WAGNER.

of the senior author, *C. ellioti* was one of the species with the highest observed density. Only two years later it was very difficult to find them (P. HITA-GARCIA pers. comm.). This was also corroborated by SPAWLS et al. (2002) and SCHMIDT et al. (2000) who also indicate that *C. ellioti* has large population density dynamics. This chameleon was found in the surrounding areas of Kakamega and Nandi forests, and also inside the forest, on the shore of the Isiukhu River. Habitats were as follows: grassland, banana and guava plantations, gardens, hedges, bushes, small trees, secondary and riverside forest.

Rhampholeon boulengeri Steindachner, 1911

1911 *Rhampholeon boulengeri* Steindachner, Anz. Akad. Wiss., Wien, 48: 178.

Specimens examined. NMK L/249, L/7270, L/2651, ; ZFMK 54021-24, 77456, 81999.

Remarks: *R. boulengeri* is a typical dweller of the East African rain forests from the eastern parts of the DR Congo in the west to Kenya in the east. Here it is, apart from Kakamega and Nandi forests, also found in the Cherangani Mts. (SPAWLS et al. 2002). Within Kakamega Forest the pygmy chameleon was found in the northern part of the main fragment and in the Kisere fragment.

Gekkonidae Oppel, 1811

Cnemaspis africana (Werner, 1895)

1895 *Gymnodactylus africanus* Werner, Verh. zool.-bot. Ges. Wien 45: 190, pl. V, fig. 5.

Specimens examined. NMK L/1987; ZFMK 82022.

Remarks: This taxon is endemic to eastern Africa and is only distributed in Kenya and Tanzania. Next to Kakamega Forest, the lizard is only known from Taita and Shimba Hills and Athiplain. ZFMK 82022 was collected in a pitfall trap near the Buyangu Hill. This suggests that *C. africana* is not a strict tree dweller but also inhabits leaf litter during its search for food.

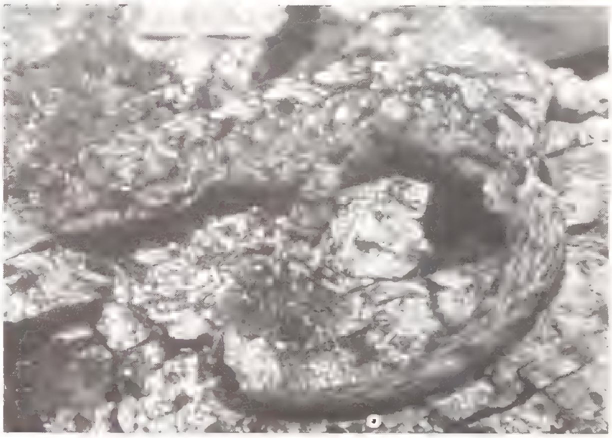

Fig. 13. *Cnemaspis elgonensis* from Kakamega Forest. Photo by Philipp WAGNER.

Cnemaspis elgonensis Loveridge, 1935

1935 *Cnemaspis elgonensis* Loveridge, Proc. Zool. Soc. London 1935: 820.

Specimens examined. NMK L/1129, L/2263; ZFMK 82023.

Additional specimens. USNM 158923.

Remarks: *C. elgonensis* is endemic to Uganda and Kenya and has a very restricted distribution area from the Mt. Elgon range to Kakamega in the south. Nothing is known about its biology but similarities with other species of the genus can be anticipated. ZFMK 82023 was found at dawn on the lavatory of Udo´s Campsite in the northern part of the forest.

Hemidactylus mabouia (Moreau de Jonnes, 1818)

1818 *Gekko mabouia* Moreau de Jonnes, Bull. Scient. Soc. Philomath. Paris, sér 3,5: 138.

Specimens examined. NMK L/2648/1-2, L/2659/1, L/2659/3-4; ZFMK 70833-34, 81982-86.

Remarks: This species inhabits nearly the entire sub-Saharan Africa. It has been transported by humans to South America (DIRKSEN 1995), Florida, USA (POWELL et al. 1998), Madagascar (GLAW & VENCES 1994) and to Madeira, Portugal (JESUS et al. 2002). In Kakamega it inhabits the houses of the villages around the forest and also of Kakamega town. No specimens were found outside of human habitations.

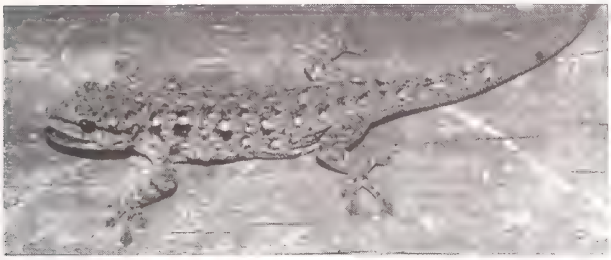

Fig. 14. *Lygodactylus gutturalis* from Kakamega Forest. Photo by Jörn Köhler.

Lygodactylus gutturalis (Bocage, 1873)

1873 *Hemidactylus gutturalis* Bocage, J. Sci. math. phys. nat. Lisboa 4: 211.

Specimens examined. NMK L/2464; ZFMK 81987.

Remarks: This is the first record of the species for Kenya. The geographically closest record is from the Ugandan side of Mt. Elgon. *L. gutturalis* is a typical species of the equatorial rain forest and is distributed from Senegal in the west to Kenya in the east. As it is the case in several other forest species with the same distribution pattern (e. g. *Lepidothyris fernandi* species complex: Wagner et al. subm.), the East African populations might prove to be a new taxon. NMK L/2464 was found inside a tent on Udo´s Campside.

Scincidae Oppel, 1811

Eumecia anchietae Bocage, 1870

1870 *Eumecia anchitae* Bocage, J. Sci. Lisboa 3: 66-68.

Specimens examined. NMK L/110/1+2, L/2657, L/2669; ZFMK 75069, 76044, 81981.

Remarks: This species was found in several habitats, e. g. urban areas inside the villages and Guava dominated secondary structures. ZFMK 81981 was found on a tree (Strychnaceae: *Strychnus* cf. *usambarensis*), which was very slanting and shaggy with ferns and mosses, so this sighting was presumable an exception of this normally ground-dwelling species.

Feylinia currori Gray, 1845

1845 *Feylinia currori* Gray, Catalogue of the lizards of the British Museum, p. 129.

Specimens examined. NMK L/2662; ZFMK 81998.

Key references: Wagner & Schmitz 2006.

Remarks: These specimens were the first records of this species and genus in Kenya (Wagner & Schmitz 2006). They were found crossing a road (ZFMK 81998) and in leaf litter (NMK L/2662). A morphological comparison between east and west African populations results in no geographic directed differences (Wagner & Schmitz 2006).

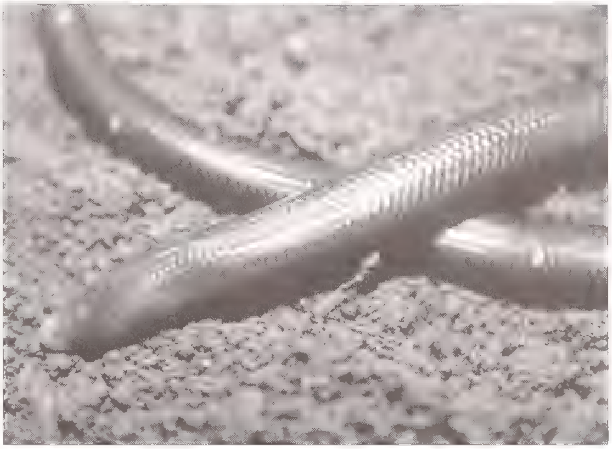

Fig. 15. *Feylinia currori* from Kakamega Forest. Photo by Philipp Wagner.

Lepidothyris aff. *fernandi* (Burton, 1836)

1836 *Tiliquia fernandi* Burton, Proc. Zool. Soc. London 1836: 62.

Specimens examined. NMK L/2147.

Key references: Wagner et al. (subm.).

Remarks: This secretive skink is probably the rarest reptile of the forest. It is only recorded by one voucher specimen and from one sighting (S. Schick, pers. comm.) in 2002. This typical equatorial rain forest species complex is distributed from Sierra Leone in the west to Kenya in the east and is currently portioned into several taxa (Wagner et al. subm.). The East African populations inhabit the forests of the eastern DR Congo to Kenya, southwards to Zambia and south-westwards to Congo and Angola. The single specimen was found in a pitfall trap next to Buyangu Hill. Also the visual record was on a forest path within this area.

Afroablepharus wahlbergi (Smith, 1849)

1849 *Cryptoblepharus wahlbergi* Smith, Illus. zool. S. Africa, 3, App. p.10.

Specimens examined. None.

Additional specimens. MCZ 41601-10, 41614-7.

Key references: Loveridge 1936.

Remarks: The vouchers were collected by Loveridge (1936) at Kaimosi area and he remarked that most of the collected female specimens were pregnant in February.

Trachylepis maculilabris (Gray, 1845)

1845 *Euprepis maculilabris* Gray, Catalogue of the lizards of the British Museum.

Specimens examined. None.

Additional specimens. CAS 122720, 122723; USNM 49203.

Key references: DREWES 1976.

Remarks: The material from CAS was collected by DREWES (1976) in Kaimosi area. Since then no other vouchers were collected.

Trachylepis megalura (Peters, 1878)

1878 *Euprepis megalurus* Peters, Monatsber. Akad. Wiss. Berlin, p. 204.

Specimens examined. NMK L/1915/1-2; ZFMK 81997.

Additional specimens. CAS 122728; USNM 49066-68, 49199.

Remarks: Only a single specimen was found during the survey 2003 on a slope of the Liranda Hill in the southern part of the forest. This habitat is dominated by grassland with sporadic trees. The only other reptile species recorded on this hill in rocky areas was *T. quinquetaeniata*. DREWES (1976) found the taxon also on clearings in the Buyangu area.

Trachylepis quinquetaeniata (Lichtenstein, 1823)

1823 *Scincus quinquetaeniatus* Lichtenstein, Verzeichnis der Dubletten, Berlin, p. 103.

Specimens examined. NMK L/2650/2-3, 2650/5, 2656/2-3; ZFMK 81988-93, 81995-96, 82060-61.

Additional specimens. CAS 122709-719, 122721-722.

Remarks: The species shows a disjunct distribution within the Kakamega area. It is only found in rocky areas of the Buyangu and Liranda Hill as well as on a small hill near Kisere. No specimens were found on houses, bridges or other human buildings as it was described by SPAWLS et al. (2002). Also DREWES (1976) found the specimens on exposed rocks. FINK (2003) has shown that the diet is dominated by isopod species, but also molluscs were found.

Trachylepis striata (Peters, 1844)

1844 *Tropidolepisma striatum* Peters, Berl. Bekanntmach. Geeignet. Verhandl. Königl.-Preuss. Akad. Wiss. Berlin 1844: 32-37.

Specimens examined. NMK L/2654/2, 2654/5; ZFMK 70825-30, 82002-06, 82011-21.

Additional specimens. CAS 122724-727; USNM 49069-71, 49207-16, 49389, 49393.

Remarks: *T. striata* is one of the species with the highest density in Kakamega area and was found everywhere outside the forest or wooded areas. But meanwhile the species has reached the BIOTA Camp, located on a small clearing of Udo´s Campside inside the forest. Here and on the houses of the near villages it is sympatric with *Adolfus jacksoni* (Lacertidae) and only on the houses also with *Acanthocercus atricollis* (Agamidae). In contrast to the data given by RAZZETTI & MSUYA (2002) and SPAWLS et al. (2002), *T. striata* was never found on trees or in plantations. The diet analysed by FINK (2003) is dominated by Coleoptera and also consists of other winged insects, collembolans, spiders, nematodes and molluscs.

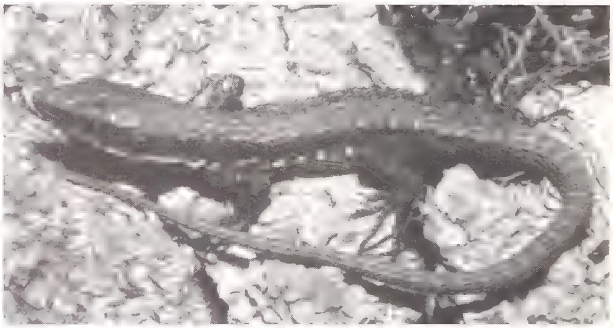

Fig. 16. *Adolfus africanus* from Kakamega Forest. Photo by Philipp WAGNER.

Lacertidae Oppel, 1811

Adolfus africanus (Boulenger, 1906)

1906 *Algiroides africanus* Boulenger, Proc. Zool. Soc. London 2: 570-572.

Specimens examined. NMK L/2661/2; ZFMK 77457, 81205-07.

Key references: KÖHLER et al. 2004.

Remarks: These specimens were the first record of the species for Kenya (KÖHLER et al. 2004). As a typical inhabitant of the equatorial rainforest, *A. africanus* has a disjunct distribution from Cameroon in the West to Kenya in the East, but taxonomic comparisons have shown that there are no geographic directed differences between the populations (KÖHLER et al. 2004) and no subspecies are recognizable. Most of the vouchers were collected in a pitfall trap near the Buyangu Hill. ZFMK 81207 was collected by hand in a secondary guava forest, the Salazar Circuit. ZFMK 77457 was collected in the southern part of the forest near Isecheno by W. FREUND and J. KÖHLER in 2002.

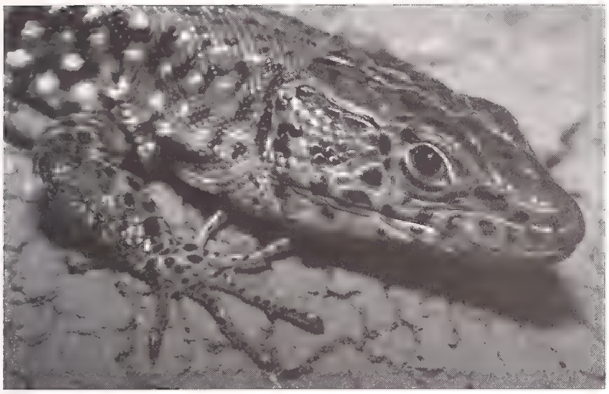

Fig. 17. *Adolfus jacksoni* from Kakamega Forest. Photo by Jörn Köhler.

Adolfus jacksoni (Boulenger, 1899)

1899 *Lacerta jacksoni* Boulenger, Proc. Zool. Soc. London 1: 96-98.

Specimens examined. PW 04 & PW 05 (now part of the NMK collection); ZFMK 70831-32, 81964-73.

Additional specimens. CAS 122729-30, 141566, 147904.

Key references: Spawls & Rotich 1997.

Remarks: *A. jacksoni* was recorded for Kakamega Forest by Spawls & Rotich (1997) for the first time. Most of the specimens were collected in the Biota Camp and in forest surrounding villages. No specimens were found in gardens or small plantations but they were sighted on trees within maize and cane fields. Only one specimen was sighted near to the forest inside the Salazar Circuit. In contrast to the data provided by Razzetti & Msuya (2002), *A. jacksoni* was rarely seen climbing on trees. The diet consists mainly of Isoptera, Orthoptera and Lepidoptera, but also of other arthropods.

Cordylidae Mertens, 1937

Chamaesaura anguina (Linnaeus, 1758)

1758 *Chamaesaura tenuior* Linnaeus, Systema Naturae. 10th edition.

Specimens examined. NMK L/2020.

Remarks: The specimen was collected in 1992 probably in the southern part of the forest. Further data are not available. Because of the distribution this specimen was assigned by use to the subspecies *tenuior*.

Varanidae Hardwicke & Gray, 1827

Varanus aff. *niloticus* (Linnaeus, 1766)

1766 *Lacerta nilotica* Linnaeus, Syst. Nat. Ed. 12 (1): 369.

Specimens examined. None.

Remarks: This species is known only from literature and sightings (Loveridge 1936; Mertens 1942). The details of the specimens seen are unknown. Specimens were sighted (by the first author and by J. Köhler, pers. comm.) on the shore of the Isiukhu River near Buyangu village. It remains to be shown whether the Kakamega population belongs to *V. niloticus* or *V. ornatus*. The fact that Kakamega Forest is a remnant of the equatorial rain forest makes the existence of *V. ornatus* possible. The nearest locality documented by a voucher specimen is Kisumu (NMK L/2476), but this is a typical habitat for *V. niloticus*. Also Analo (2003) refers to the occurrence of *Varanus niloticus* in the Kakamega area and reported that the skin is used for traditional drums.

Typhlopidae Merrem, 1820

Typhlops angolensis (Bocage, 1866)

1866 *Onychocephalus angolensis* Bocage, Jorn. Sci. Math. Phys. Nat. Lisboa 1: 46, 65.

Specimens examined. None.

Remarks: This taxon is known only from literature (Loveridge 1935) and further data were not available.

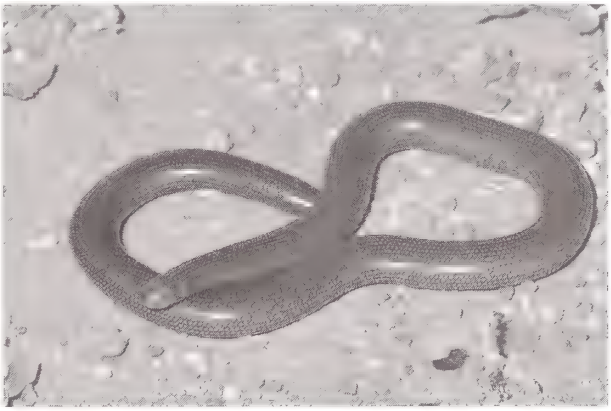

Fig. 18. *Typhlops lineolatus* from Kakamega Forest. Photo by Mike Dobiey.

Typhlops lineolatus Jan, 1864

1864 *Typhlops lineolatus* Jan, Iconogr. Gén. Ophid. 1(9. livr.): 5.

Specimens examined. PW 157 & 162 (now part of the NMK collection); ZFMK 73283, 82051-52.

Remarks: Most of the vouchers were collected after rainfall on Udo´s Campsite. One specimen (ZFMK 82051) was from Buyangu village and collected in a grassy area on a rainy day.

Colubridae Oppel, 1811

Crotaphopeltis hotamboeia (Laurenti, 1768)

1768 *Coronella hotamboeia* Laurenti, Syn. Rept.: 58.

Specimens examined. NMK O/2691

Remarks: Further data on the NMK specimen is not available, but one specimen was sighted at Salazar Circuit.

Dasypeltis atra Sternfeld, 1912

1912 *Dasypeltis scabra* var. *atra* Sternfeld, IV. Zool. II Lfg. Reptilia, in: Schubotz: Wiss. Ergeb. Deut. Zentr. Afr. Exp.: 197-279.

Specimens examined. MHNG 1.262.072-075; NMK S/2576; ZFMK 77459, 82054.

Additional specimens. CAS 142248.

Remarks: Spawls et al. (2002) noted that completely black specimens have been collected east of the Rift Valley. So, ZFMK 82054 is probably the first melanistic voucher from west of the Rift Valley. However, ZFMK 77459 demonstrates sympatric occurrence of the light colour phase with the melanistic one.

Dasypeltis scabra (Linnaeus, 1758)

1758 *Coluber scaber* Linnaeus, Syst. Nat. Ed. 10(1): 824.

Specimens examined. ZFMK 75070.

Additional specimens. USNM 49376.

Remarks: Further data are not available, but specimens were sighted at Salazar Circuit.

Dispholidus typus Smith, 1829

1829 *Bucephalus typus* Smith, Zool. Journ. 4: 433-444.

Specimens examined. NMK S/986

Remarks: This specimen is assigned to the subspecies *kivuensis*, because of its distribution from west of the Rift Valley in Kenya to Rwanda in the east and Zambia in the south. Further data are not available, but one specimen was sighted by the senior author in secondary forest at the Salazar Circuit.

Hapsidophrys lineatus Fischer, 1856

1856 *Hapsidophrys lineatus* Fischer, Abhandl. Nat. Ver. Hamburg 3 (4): 81-116.

Specimens examined. NMK O/2715; ZFMK 82053.

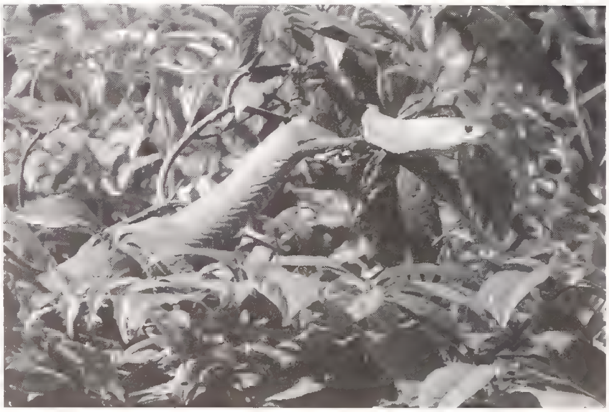

Fig. 19. *Dispholidus typus* from Kakamega Forest. Photo by Mike Dobiey.

Additional specimens. CAS 147910-11, 147913, 150987, 153222.

Remarks: This species which is typical for the equatorial rainforest, is distributed from Guinea-Bissau in the west to Kenya in the east and taxonomic analyses did not show geographic directed differences between the populations. ZFMK 82053 was found basking on a bush next to a small pond in the Buyangu area.

Lamprophis fuliginosus (Boie, 1827)

1827 *Lycodon fuliginosus* Boie, Isis van Oken 20, col. 551.

Specimens examined. NMK S/3981/1-2; ZFMK 82037-43.

Additional specimens. CAS 122743, 141529.

Remarks: All vouchers were collected inside the houses or gardens of Buyangu Village.

*Lycophidion capense (*Smith, 1831)

1831 *Lydodon capensis* Smith, S. Afr. Quart. J.. 1: 18.

Specimens examined. None.

Additional specimens. CAS 122741.

Remarks: Further data are not available. The specimen is catalogued at CAS as *L. c. capense* Boulenger, 1893.

Lycophidion depressirostre Laurent, 1968

1968 *Lycophidion depressirostre* Laurent, Bull. Mus. Comp. Zool., Harv. 136 (12): 472.

Specimens examined. None.

Additional specimens. USNM 49388.

Remarks: Further data are not available.

Lycophidion ornatum Parker, 1936

1936 *Lycophidion ornatum* Parker, Novit. Zool. 40: 122.

Specimens examined. ZFMK 75071, 82044.

Additional specimens. BMNH 1962.819; MCZ 40471-73.

Remarks: *L. ornatum* has a wide distribution from Nigeria in the West to Mt Kenya in the East. ZFMK 82044 was found in twilight inside the forest.

Mehelya capensis (Smith, 1847)

1847 *Heterolepis capensis* Smith, Illustrations of the zoology of South Africa, Reptilia.

Specimens examined. None.

Additional specimens. CAS 150988.

Remarks: This voucher is catalogued at CAS as *M. c. savorgnani* Mocquard, 1887. Further data are not available.

Natriciteres olivacea (Peters, 1854)

1854 *Coronella olivacea* Peters, Monatsber. Königl. Akad. Wiss. Berlin 1854: 614-628.

Specimens examined. ZFMK 82035.

Remarks: *N. olivacea* inhabits water bodies in bushland and savannah regions. In contrast to the described habitats (e. g. Spawls et al. 2002; Marais 2004), our specimen was collected basking on dense vegetation on the shore of the Isiukhu inside the northern part of the forest. But there is another specimen collected inside a forest by Ullenbruch (2003) in Benin.

Philothamnus battersbyi Loveridge, 1951

1951 *Philothamnus irregularis battersbyi* Loveridge, Bull. Mus. Comp. zool. Harvard 106: 51.

Specimens examined. NMK S/3986, S/3992; ZFMK 82048.

Additional specimens. CAS 150978-980, 153223.

Remarks: *Philothamnus* is probably one of the most difficult, for the taxonomists, reptile genera in Africa. But *P. battersbyi* is relatively easy to identify by the uniform green colouration, two supralabials entering the eye, a divided anal scale, 15 midbody scale rows and no keels on the subcaudal scales. It can only be confused with the likewise uniform green *P. angolensis*. Most vouchers collected within the study were found in Buyangu Village basking on small bushes. One was found killed on the road.

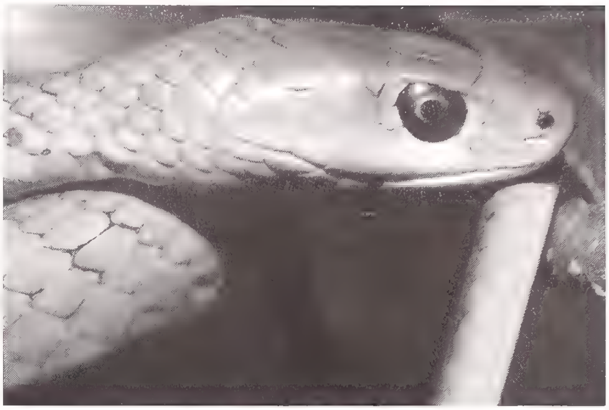

Fig. 20. *Philothamnus battersbyi* from Kakamega Forest. Photo by Philipp Wagner.

Philothamnus carinatus (Andersson, 1901)

1901 *Chlorophis carinatus* Andersson, Bihang Till. K. Sv. Vet.- Akad. Handl. 27 (5): 9.

Specimens examined. None.

Remarks: This taxon is only recorded from literature (Hughes 1985; Spawls et al. 2002).

Further data are not available.

Philothamnus heterolepidotus (Günther, 1863)

1863 *Ahaetulla heterolepidota* Günther, Ann. Mag. Nat. Hist. 11 (3): 286.

Specimens examined. NMK S/65-66, S/68, S/120-123.

Remarks: The vouchers were not collected in the area close to Kakamega Forest but on the shores of the Yala River in the Siaya District. The Yala also crosses the southern part of the Kakamega Forest. In view of this, the occurrence of the species in the Kakamega area is likely.

Philothamnus hoplogaster (Günther, 1863)

1863 *Ahaetulla hoplogaster* Günther, Ann. Mag. Nat. Hist. 11 (3): 284.

Specimens examined. None.

Remarks: This taxon is only recorded from literature (Hughes 1985; Spawls et al. 2002).

Further data are not available.

Philothamnus nitidus Günther, 1863

1863 *Ahaetulla nitida* Günther, Ann. Mag. Nat. Hist. (3) 11: 283-287.

Specimens examined. NMK S/67, S/69.

Remarks: The vouchers were not collected in the area close to Kakamega Forest but on the shores of the Yala River in the Siaya District. The river crosses the southern part of the Kakamega Forest (see *P. heterolepidotus* above). After closer examination, NMK S/67 & S/69 were assigned to the subspecies *P. n. loveridgei* Laurent, 1960.

Psammophis mossambicus Peters, 1882

1882 *Psammophis mossambicus* Peters, Reise nach Mossambique, p. 122.

Specimens examined. NMK S/2316, S/2319; ZFMK 82049.

Key references: SPAWLS et al. 2002.

Remarks: SPAWLS et al. (2002) placed the eastern populations of *P. phillipsi* and *P. sibilans* in the synonymy of *P. mossambicus*. Examination of the type material of *P. mossambicus* support this decision but it has to be kept in mind that the earlier recognized *P. phillipsi* is a relatively small sized rainforest species with an entire anal scale (STERNFELD 1907; LOVERIDGE 1940; VILLIERS 1975; TAYLOR & WEYER 1958; DOUCET 1963; CHIPPAUX 2001). The voucher ZFMK 82049 was found inside Buyangu Village, basking on a small bush.

Psammophis phillipsi (Hallowell, 1844)

1844 *Coluber phillipsi* Hallowell, Proc. Acad. Nat. Sci. Philadelphia 1844: 169.

Specimens examined. NMK O/3603; ZFMK 82050.

Key references: CHIPPAUX 2001.

Remarks: These vouchers represent the first record of the species for Kenya. For the taxonomic assignment see *P. mossambicus*. SPAWLS *et al.* (2002) placed the eastern populations of *P. phillipsi* and *P. sibilans* in the synonymy of *P. mossambicus*. ZFMK 82050 was found 100 m away from a pond inside the primary forest of the Buyangu area. The second voucher was collected on the Buyangu Hill, a natural clearing inside the forest.

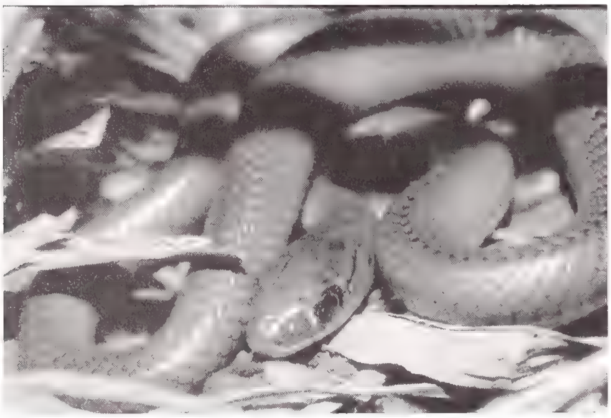

Fig. 21. *Psammophis phillipsi* from Kakamega Forest. Photo by Jörn KÖHLER.

Psammophis rukwae Broadley, 1966

1966 *Psammophis sibilans rukwae* Broadley, Arnoldia Rhod. 2 (36): 3.

Specimens examined. None.

Remarks: This taxon is only known from literature (SPAWLS et al. 2002). Further data are not available.

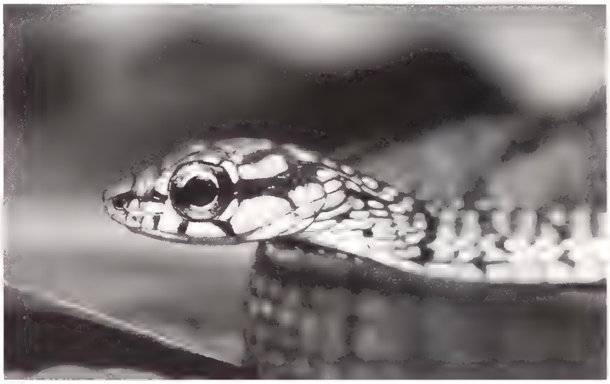

Fig. 22. *Thrasops aethiopissa* from Kakamega Forest. Photo by Philipp WAGNER.

Thrasops aethiopissa (Günther, 1862)

1862 *Rhamniophis aethiopissa* Günther, Ann. Mag. nat. Hist. (3) 9: 124-132.

Specimens examined. NMK O/3563; ZFMK 76045, 77290, 82032.

Additional specimens. CAS 147909, 152794.

Remarks: *T. aethiopissa* is a typical rain forest species whose East African populations are assigned to the subspecies *T. a. elgonensis* (LOVERIDGE, 1929) which is only known from the Mt. Elgon and Kakamega forests in Kenya. ZFMK 82032 was collected at daytime basking on a 20 cm high bush on a clearance of the Buyangu area. When threatened it displays typical defence behaviour similar to the boomslang.

Thrasops jacksonii Günther, 1895

1895 *Thrasops jacksonii* Günther, Ann. Mag. Nat. Hist. 15 (6): 523-529.

Specimens examined. MHNG 1.375.038-040, 042; ZFMK 66275-76, 68516.

Additional specimens. CAS 122295, 152795.

Remarks: Details on the vouchers are unknown.,

Toxicodryas blandingii (Hallowell, 1844)

1844 *Dipsas blandingii* Hallowell, Proc. Acad. Nat. Sci. Philad. 1844: 170.

Specimens examined. MHNG 1.356.058.

Additional specimens. CAS 150981-82.

Remarks: In Kenya it is only known from Kakamega Forest and the Serem area. Further data are not available.

Toxicodryas pulverulenta (Fischer, 1856)

1856 *Dipsas pulverulenta* Fischer, Abhandl. Nat. Ver. Hamburg 3 (4): 81-116.

Specimens examined. None.

Additional specimens. CAS 122742.

Remarks: Further data are not available..

Atractaspididae Günther, 1858

Polemon christyi (Boulenger, 1903)

1903 *Miodon christyi* Boulenger, Ann. Nat. Hist. (7) xii : 354.

Specimens examined. None.

Additional specimens. CAS 147905.

Remarks: Details on this voucher are unknown.

Elapidae Boie, 1827

Dendroaspis jamesoni Traill, 1843

1843 *Elaps jamesoni* Traill, Edinburgh new. phil. J., 34 (67): 54.

Specimens examined. MHNG 1327.046-48; ZFMK 82036.

Additional specimens. CAS 122298-99.

Key references: Loveridge 1936.

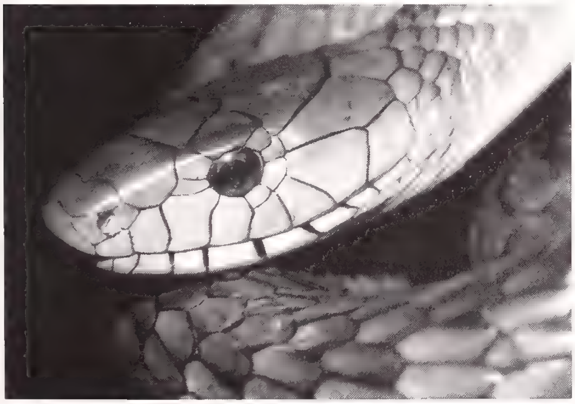

Fig. 23. *Dendroaspis jamesoni kaimosae* from Kakamega Forest. Photo by Philipp Wagner.

Remarks: *D. jamesoni* is distributed from Ghana in the west to Kenya in the east and southwards to Angola. In Kenya, the subspecies *D. j. kaimosae* Loveridge, 1936 (with the type locality Kaimosi) is hitherto recorded from Kenya by vouchers from Kakamega Forest, and a sighting from Lolgorien, Mara Escarpment (Spawls et al. 2002). During the course of this study we found a voucher specimen (NHMW 28109) collected from Nakuru. ZFMK 82036 was found on the shore of the Isiukhu River in the northern part of the forest, basking on a horizontal branch at about midday.

Elapsoidea loveridgei (Parker, 1949)

1949 *Elapsoidea sundevalli loveridgei* Parker, Zool. Verh. Leiden 6: 1-115.

Specimens examined. MHNG 1328.010; ZFMK 82001.

Additional specimens. CAS 152796.

Remarks: ZFMK 82001 was found in the morning after a rainy night; it was crossing the forest road near to the Buyangu gate. After examination of the vouchers they were assigned to the subspecies *E. l. multicincta* (Laurenti, 1956) however the nominate form *E. l. loveridgei* also occurs in Kenya east of the Rift Valley.

Naja melanoleuca Hallowell, 1857

1857 *Naja haie* var. *melanoleuca* Hallowell, Proc. Acad. Nat. Sci. Philadelphia 1857: 61.

Specimens examined. NMK S/3980, S/3985; ZFMK 82045-47.

Additional specimens. CAS 122749, 122758.

Remarks: *N. melanoleuca* is the most common venomous snake in the Kakamega area. Snakes were found in several habitats and areas, e. g. inside the forest: near the Isiukhu Falls, near the Buyangu Gate, south of Udo´s Campside, Yala River, Kaimosi fragment and Malava fragment; outside the forest (mostly juveniles) within Buyangu Village, Isecheno and Salazar Circuit (both sightings).

Pseudohaje goldii (Boulenger, 1895)

1895 *Naia goldii* Boulenger, Ann. Mag. Nat. Hist. London 16 (6): 34.

Specimens examined. NMK S/3366

Remarks: This species has a wide but disjunct distribution from Togo (Hughes & Barry 1969) in the west to Kenya in the east and southwards to Angola and Namibia (Obst et al. 1988). In Kenya it is only known from Kakamega Forest but the occurrence in the Mt. Elgon forests is possible. Further data are not available.

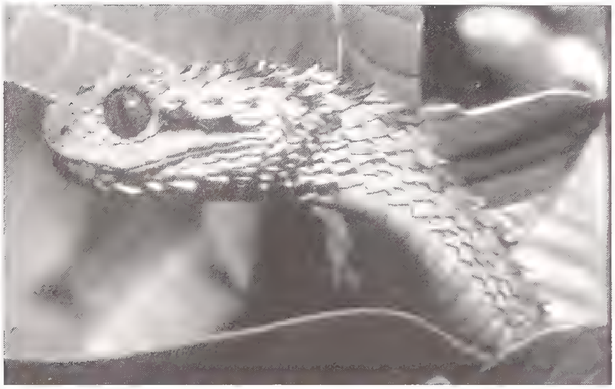

Fig. 24. *Atheris hispida* from Kakamega Forest. Photo by Philipp Wagner.

Viperidae Laurenti, 1768

Atheris hispida Laurent, 1955

1955 *Atheris hispidus* Laurent, Rev. Zool. Bot. Afr. 51: 138.

Specimens examined. MHNG 2236.23; NMK O/1648; NMZB-UM 5317; ZFMK 66374, 82024-26.

Additional specimens. CAS 141750, 147906, 147908.

Remarks: This bush viper is only known in Kenya from the Kakamega Forest, where it is sympatric with *A. squamigera*. Spawls et al. (2002) stated that *A. hispida* inhabits higher and drier bushes than *A. squamigera* which does not seem to be the case in Kakamega Forest, where *A. hispida* was found mostly in low elevation of a maximum of 80 cm. Spawls et al. (2002) also reported that the taxon was never collected in Kakamega since the early 1990´s, so that this record is the rediscovery of the species there. Most vouchers were collected in the northern part of the forest. Only CAS 122747 was found in the Kaimosi fragment.

Atheris squamigera (Hallowell, 1854)

1854 *Echis squamigera* Hallowell, Proc. Acad. Nat. Sci. Philadelphia 1854: 193.

Specimens examined. PW 158 & 163 (now part of the NMK collection); ZFMK 64337-42, 81214, 82027, 82029.

Additional specimens. CAS 122744-46, 122748, 147902-03, 148629, 150983-84, 153468; NMZB-UM 5393, 6518-19.

Remarks: *A. squamigera* is a common viper inside Kakamega Forest, where it occurs sympatrically with *A. hispida*. Most vouchers were collected in the northern part of the forest. Only Drewes collected two specimens 1969 near Kaimosi in the southern part of the forest. *A. squamigera* has a disjunct distribution from Ghana (Hughes & Barry 1969) in the west to Kenya in the east, southwards to Angola and Tanzania. Additionally studies may demonstrate differences between the populations. In Kenya *A. squamigera* is, with two exceptions, only known from Kakamega Forest. Two records are from outside the forest: one specimen from Chemilil and one sighting from the Soit Ololol Escarpment (Spawls et al. 2002). Specimens collected in this study were exclusively found near water bodies in the Buyangu area. They were found by hunting by torchlight and basking on small bushes or in leaf litter at daytime.

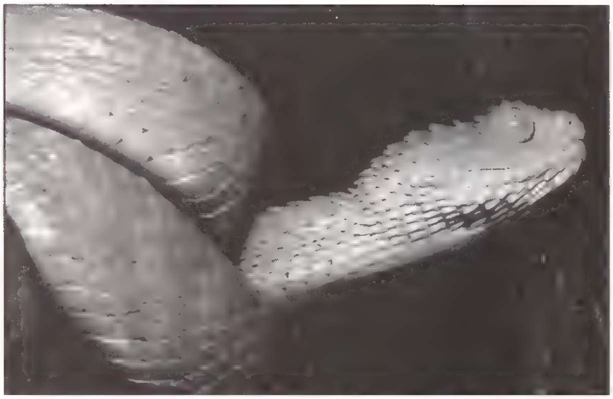

Fig. 25. *Atheris squamigera* from Kakamega Forest. Photo by Jörn Köhler.

Bitis gabonica (Dumeril, Bibron & Dumeril, 1854)

1854 *Echidna gabonica* Dumeril, Bibron & Dumeril, Erpét. Gén. 7: 1428.

Specimens examined. NMK S/2904

Remarks: Details on this record are unknown, but several sightings of the taxon are reported from the grassland near the entrance of Udo´s Campsite and from the Salazar Circuit. In Kenya this taxon is only known from the Kakamega and Nandi areas.

Bitis nasicornis (Shaw, 1802)

1802 *Coluber nasicornis* Shaw, Nat. Misc. 3, pl. 94.

Specimens examined. NMK S/3978; ZFMK 82030-31.

Additional specimens. CAS 150989, 150990.

Remarks: Like the previous species also *B. nasicornis* was often found and sighted on the roads of the Salazar Circuit. Also this taxon occurs within Kenya only at the Kakamega and Nandi areas. Two vouchers (ZFMK 82030 and 82031) were found near the Isiukhu Falls. The stomach of ZFMK 82031 contained (Muridae: *Lophuromys laticeps*) as prey item.

Causus lichtensteini (Jan, 1859)

1859 *Aspideplaps lichtensteini* Jan, Rev. & Mag. Zool. 1859: 511.

Specimens examined. NMK S/2499; ZFMK 82033-34.

Additional specimens. CAS 154579.

Remarks: This forest species has a wide distribution from Côte d'Ivoire in the west (Rödel & Mahsberg 2000) to Kenya in the east and southwards to Zambia (Broadley et al. 2003). In Kenya this taxon is only known from the Kakamega and Nandi areas. All vouchers of the study are juveniles and were collected after rainfall in the evening in the grassland near Udo´s Campsite and in the morning at the forest border and in Guava bushland in the Buyangu area.

Causus resimus (Peters, 1862)

1862 *Heterophis resimus* Peters, Monatsber. Akad. Wiss. Berlin 1862: 271-279.

Specimens examined. None.

Remarks: This taxon is only recorded from literature (Pitman 1974). Further data are not available.

Testudines

Pelomedusidae Cope, 1868

Pelomedusa subrufa (Lacépède, 1788)

1788 *Testudo subrufa* Lacépède, Hist. nat. Quadrup. Ovip. Synops. Method. 1: 173, pl. 12.

Specimens examined. NMK C/53; ZFMK 81951.

Remarks: Interestingly this typical savannah species was also found inside the forest. Several adult specimens were found inside a pond in the Buyangu area. Juveniles were found in smallest water bodies inside and outside the forest e. g. in small temporary stream on the Buyangu Hill. But *P. subrufa* was also found in the surrounding area, in fish and garden ponds. Specimens were also sighted on the shores of the Isiukhu River, but not at the Yala River.

4.2. KEY TO THE SPECIES

Amphibians

1	- Tongue absent.	**Pipidae** *Xenopus victorianus*
	- Tongue present.	**2**
2	- Upper jaw toothless	**Bufonidae (5)**
	- Upper jaw with teeth.	**3**
3	- Fine dorsal skin ridge along midline.	**Arthroleptidae (6)**
	- Dorsal skin ridge absent.	**4**
4	- Last phalanx of fingers out of alignment.	**Hyperoliidae (7)**
	- Last phalanx of fingers not out of alignment.	**Ranidae (10)**
5	- Parotoid glands distinct and raised.	*Amietophrynus kisoloensis*
	- Parotoid glands indistinct and flattened.	*Amietophrynus maculatus*
6	- Heels (tarsus) black with thin white border in males.	*Leptopelis mackayi*
	- Heels lacking this pattern in males.	*Leptopelis* aff. *bocagii*
7	- Pupil horizontal to round.	***Hyperolius***
	- Pupil vertical.	**8**
8	- Vomerine teeth absent.	***Afrixalus* (9)**
	- Vomerine teeth present.	***Kassina*** *Kassina senegalensis*
9	- Thin pale marking from the lower back around a dark rectangular patch anteriorly.	*Afrixalus osorioi*
	- This particular pattern absent.	*Afrixalus quadrivittatus*

10	- Vomerine teeth absent.	***Phrynobatrachus* (18)**
	- Vomerine teeth present.	**11**
11	- Vomerine projections between internal nostrils.	**12**
	- Vomerine projections abutting onto anterior margins of internal nostrils	***Ptychadena* (14)**
12	- Transverse skin groove behind the eyes.	*Hoplobatrachus occipitalis*
	- Transverse skin groove absent.	**13**
13	- Golden to brownish band from snout to vent.	*Amnirana albolabris*
	- Band absent.	*Afrana angolensis*
14	- Pale triangle on snout.	**15**
	- Pale triangle absent.	**16**
15	- Distance from nostril to snout greater than internarial distance.	*Ptychadena oxyrhynchus*
	- Distance from nostril to snout not more than internarial distance.	*Ptychadena anchietae*
16	- 2 to 2 1/3 phalanges of fourth toe free of web.	*Ptychadena mascariensis*
	- 2.5 phalanges or more on fourth toe free of web.	**17**
17	- Back of thigh spotted or mottled.	*Ptychadena porossima*
	- Back of thigh with and dark longitudinal bands.	*Ptychadena taenioscelis*
18	- Tympanum visible.	**19**
	- Tympanum not visible.	*Phrynobatrachus* aff. *mababiensis*
19	- Discs on fingers absent.	*Phrynobatrachus natalensis*
	- Discs on fingers very small, only swellings.	*Phrynobatrachus graueri*

TERRAPINS

1	Only terrapin in Kakamega area	*Pelomedusa subrufa*

LIZARD FAMILIES

1	- Head dorsally covered with granular, small and irregular scales.	**2**
	- Head dorsally covered with large scales.	**5**
2	- Eyelids absent.	**GEKKONIDAE**
	- Eyelids present.	**3**
3	- Head much wider than neck, with clusters of spiny scales around the ear; tongue short and broad.	**AGAMIDAE**
	- Head only slightly wider than neck; tongue long and slender.	**4**
4	- Tongue very long and telescopic; digits fused together.	**CHAMAELEONIDAE**
	- Tongue long and forked; digits separate.	**VARANIDAE**
5	- Dorsal and ventral scales similar, mostly smooth.	**SCINCIDAE**
	- Ventral scales rectangular, larger than dorsals.	**6**
6	- Lateral granular fold present.	**LACERTIDAE**
	- Lateral granular fold absent.	**CORDYLIDAE** *Chamaesaura anguina*

GEKKONIDAE

1	- Pupil round.	**2**
	- Pupil vertical.	*Hemidactylus mabouia*
2	- Claws on digits except thumb present.	*Lygodactylus gutturalis*
	- Toes with a distinctive angle at the last or last two joints.	**3**
3	- Subcaudals with a continous median row; 9–12 preanal pores.	*Cnemaspis africana*
	- Subcaudals with a discontinous median row; 6–8 preanal pores.	*Cnemaspis elgonensis*

SCINCIDAE

1	- Eye covered by skin.	*Feylinia currori*
	- Eye visible.	**2**
2	- Lower eyelid with a large transparent disc.	**5**
	- Lower eyelid without a transparent disc.	**3**
3	- 2–3 digits on forelimb, 3 on hindlimb.	*Eumecia anchietae*
	- 4 or 5 digits on both limbs.	**4**
4	- Supranasals present, broadly in contact.	*Lepidothyris* aff. *fernandi*
	- Supranasals absent, if present widely separated.	*Afroablepharus wahlbergii*
5	- Scales on feet usually non-spinose and smooth.	**6**
	- Scales on feet keeled and spinose.	*Trachylepis striata*
6	- Midbody scale rows number 24–26.	*Trachylepis megalura*
	- Midbody scale rows number 28 or more.	**7**
7	- Midbody scale rows number 32–42; 5 black-bordered longitudinal stripes, blue tail in juveniles.	*Trachylepis quinquetaeniata*
	- Midbody scale rows number 30-38, without such stripes.	*Trachylepis maculilabris*

LACERTIDAE

1	- Midbody scale rows number 18–24.	*Adolfus africanus*
	- Midbody scale rows number more than 35.	*Adolfus jacksoni*

AGAMIDAE

1	- Interparietal scale not larger than the adjoining head scales.	*Acanthocercus atricollis*
	- Interparietal scale larger than the adjoining head scales.	*Agama kaimosae*

CHAMAELEONIDAE

1	- Tail short and non-prehensile.	*Rhampholeon boulengeri*
	- Tail long and prehensile.	**2**
2	- Body scalation heterogeneous.	**4**
	- Body scalation homogeneous.	**3**
3	- Occipital dermal lobes absent.	*Chamaeleo laevigatus*
	- Occipital dermal lobes present.	*Chamaeleo gracilis*
4	- Long gular crest; parietal crest very high.	*Chamaeleo hoehnelii*
	- Low crest; one or two black coloured throat grooves.	*Chamaeleo ellioti*

Snake families

1	- Eye covered by skin.	**Typhlopidae**
	- Eye not covered by skin.	**2**
2	- No poison fangs in the front upper jaw, pupil usually round.	**Colubridae**
	- Poison fangs in the front upper jaw present	**3**
3	- Poison fangs relatively short, immobile.	**Elapidae**
	- Poison fangs mobile or folding.	**4**
4	- Eye large, head dorsum covered with small scales (except *Causus*).	**Viperidae**
	- Eye tiny, head dorsum with large symmetrical scales.	**Atractaspididae**

Typhlopidae

1	- Second supralabial overlapping preocular scale.	*Typhlops angolensis*
	- Second supralabial overlapping ocular scale.	*Typhlops lineolatus*

Elapidae

1	- Midbody scales rows number 13, always with broad bands.	*Elapsoidea loveridgei*
	- Midbody scale rows number more than 13.	**2**
2	- 3 preoculars scales, head long and narrow.	*Dendroaspis jamesoni*
	- 1 or 2 preocular scales.	**3**
3	- Midbody scale rows number 15 (Rarely 17).	*Pseudohaje goldii*
	- Midbody scale rows number 19.	*Naja melanoleuca*

Viperidae

1	- Pupil round, 9 large symmetrical scales on top of the head.	**5**
	- Pupil vertical, many scales on top of the head.	**2**
2	- Subcaudal scales paired.	**3**
	- Subcaudal scales single.	**4**
3	- Long horns on the snout of the adults.	*Bitis nasicornis*
	- No or only short horns on the snout.	*Bitis gabonica*
4	- Scales strongly lanceolate on the head and front part of the body.	*Atheris hispida*
	- Scales not lanceolate.	*Atheris squamigera*
5	- Subcaudal scales single.	*Causus lichtensteini*
	- Subcaudal scales paired.	*Causus resimus*

Colubridae

1	- No venom-delivery fangs in the upper jaw.	**8**
	- One or more pairs of venom-delivery fangs in the upper jaw.	**2**
2	- Pupil vertical.	**3**
	- Pupil round.	**5**
3	- Ventrals number 141–183.	*Crotaphopeltis hotamboeia*
	- Ventrals number 195–270.	**4**
4	- Midbody scale rows number 19.	*Toxicodryas blandingii*
	- Midbody scale rows number 21–25.	*Toxicodryas pulverulenta*

5	- Dorsal scales keeled.	*Dispholidus typus*
	- Dorsal scales smooth.	**6**
6	- First 5 infralabials usually in contact with the anterior sublinguals.	*Psammophis rukwae*
	- First 4 infralabials usually in contact with the anterior sublinguals.	**7**
7	- Anal scale divided.	*Psammophis mossambicus*
	- Anal scale single.	*Psammophis phillipsi*
8	- Dorsal scales smooth.	**9**
	- Dorsal scales keeled.	**20**
9	- Nostril (naris) located with a divided or semi-divided nasal.	**10**
	- Nostril (naris) located with an entire nasal.	**18**
10	- Anal scale single.	*Lamprophis fuliginosus*
	- Anal scale divided.	**11**
11	- Midbody scale rows number 13–15, reducing to 11 posteriorly.	**12**
	- Midbody scale rows number 15–21, if 15 not reducing posteriorly.	**17**
12	- A pair of enlarged occipital scales.	*Thrasops aethiopissa*
	- No enlarged occipital scales.	**13**
13	- Anal scale single.	*Philothamnus carinatus*
	- Anal scale divided.	**14**
14	- Subcaudal scales rounded or angular, not keeled.	**15**
	- Subcaudal scales sharply angular, keeled.	*Philothamnus nitidus*
15	- Ventral scales 168-194, no concealed spots on dorsal scales.	*Philothamnus heterolepidotus*
	- Ventral scales 138-179, cryptic pattern with spots on dorsal scales.	**16**
16	- Subcaudal scales 60–104, flanks often blue.	*Philothamnus hoplogaster*
	- Subcaudal scales 88–128, no blue on the body.	*Philothamnus battersbyi*
17	- Subcaudal scales 130–155.	*Thrasops jacksoni*
	- Subcaudal scales less than 130.	*Natriciteres olivacea*
18	- Midbody scale rows number 15, not reduced before the vent.	*Lycophidion ornatum*
	- Midbody scale rows number 15, reduced before the vent.	**19**
19	- Ventral scales 153–173.	*Lycophidion depressirostre*
	- Ventral scales 170–221.	*Lycophidion capense*
20	- Midbody scale rows number 15.	**21**
	- Midbody scale rows number 21–27.	**22**
21	- Ventral scales 193–244.	*Mehelya capensis*
	- Ventral scales 150–175.	*Hapsidophrys lineatus*
22	- Fewer than 80 pattern cycles between nape and base of tail.	*Dasypeltis scabra*
	- More than 80 pattern cycles between nape and base of tail or uniform black.	*Dasypeltis atra*

5. DISCUSSION

The composition of the herpetological community is typical for a forest fragment. It includes typical forest species but also some ubiquitous and bushland species. From the 22 lizard species recorded, only seven are true forest species, and for five species Kakamega Forest is the only Kenyan locality. The situation for snakes is nearly the same: from 26 species recorded, 14 are forest dwellers; of these, 12 again have their only Kenyan occurrence here. In addition, three ubiquitous species are also confined to Kenya to the Kakamega area. The species richness of snakes in this forest and its environs is remarkable on an African scale (for comparative species numbers of African snake communities see BÖHME (1993), HERRMANN et al. (2005b) and RÖDEL & MAHSBERG (2000). The richness of forest snake species also argues for a relatively intact status of the main forest fragment which seems to be still relatively undisturbed, enabling survival for many forest species.

However, the remaining smaller fragments of Kakamega Forest have drastically reduced species richness as compared to the main fragment. From Malaba, the least intact fragment, only two forest species, viz. the toad *Amietophrynus kisoloensis* and the forest cobra *Naja melanoleuca* have been recorded. The Kisere fragment is known to have only one additional forest species, viz. *Rampholeon boulengeri*, but more forest species might be expected in this protected forest relict. The Kaimosi fragment, finally, is home for two bushviper (*Atheris*) species and the green mamba (*Dendoaspis jamesoni kaimosae*). This drastic decrease in numbers of forest-dwelling species underlines the need of effective conservation measures in order to stop any further deforestation and forest fragmentation.

BENNUN & NJOROGE (1999) characterised Kakamega Forest as a mid-altitude tropical rainforest. This view is supported by the occurrence of the (sub)montane tree fern *Cyathea manniana* which is currently found only in the Nandi Escarpment forests which lie a few hundred meters higher than Kakamega Forest. The same can be concluded from the altitudinal distribution of the forest reptiles: of 21 forest species, 18 have a mid-altitudinal distribution, but this group is dominated by 11 species assignable to lowland forests. The assignment to a lowland rather than to a montane forest is also corroborated by the bird fauna. BENNUN & NJOROGE (1999) found 194 forest species of which 40 were typical members of the Guineo-Congolian forest block. Of 134 typical Congo Basin bird species as defined by CHAPIN (1932), 37 occur in Kakamega Forest. This amount increases to 57 out of 125 when the species from lowland secondary forests and forest clearings are also taken into account. Studies of Kakamega's Lepidoptera yielded similar results (CARCASSON 1964), and also the reptiles support the view of a mid-altitude rainforest dominated by lowland species.

Several authors regarded Kakamega Forest as the easternmost outlier of the Guinea-Congolian rainforest block (ZIMMERMANN 1972; DREWES 1976; HAMILTON 1976; SCHIØTZ 1976; KOKWARO 1988; VONESH 2001; KÖHLER 2004; CLAUSNITZER 2005; SCHICK et al. 2005). The last mentioned authors have analysed the distribution of the 24 amphibian species recorded so far from Kakamega Forest. They assigned eight species to their distribution pattern type "East African Highland", seven were widely distributed forms including other parts of the equatorial rainforests and even parts of southern Africa. Five species show a typical "arid corridor" distribution (see POYNTON 1995; P. WAGNER, unpubl. data), and only four species (*Amnirana albolabris, Afrixalus osorioi, A. quadrivittatus, Hyperolius cinnamomeoventris*) exhibit a typical Guinea-Congolian distribution pattern. In this regard, the amphibian fauna of Kakamega gives a less clear picture of the geographic assignment of this forest as compared with the reptilian fauna. Comparing the latter community with that of other African rainforests (WAGNER et al. submitted.), it turns out that it shares many more species with the Bwindi and Kibale Forests in Uganda, and even with the far distant Ziama Forest in Guinea, West Africa than e. g. with the Kenyan coastal Arabuko-Sokoke Forest or even the Eastern Arc montane forests. The analysis of Kakamega's reptile fauna, therefore, clearly argues for a Guinea-Congolian assignment of the relictual Kakamega Forest.

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Appendix

Ecological characteristics of the 58 reptiles recorded within the area of the Kakamega Forest

Taxon	Abun[a]	Loc[b]	Diet[c]	Hab[d]	Act[e]	Micro[f]	Alt[g]	Distr.[h]
Testudinae								
Pelomedusa subrufa	U	2	I,A,B	W,L	D	Aq	0–1600	SSA
Sauria, Gekkonidae								
Cnemaspis africana	I	2	I	FI	N	A	0–2000	EA
Cnemaspis elgonensis	I	2	I	FI	N	A	1200–2200	EA
Hemidactylus mabouia	C	1	I	F	N	A, AP	0–2500	SSA
Lygodactylus gutturalis	R	2,5	I	FE	DN	A	700–2000	EA
Agamidae								
Acanthocercus atricollis	C	1	I	A, F	D	A, AP	0–2400	NEA
Agama kaimosae	R	7	I	L	D		1800	K
Chamaeleonidae								
Chamaeleo ellioti	C	1,2,3,4,6,7, 10,11,13	I	A,FE, F,FI	D	AL	1500–2800	CE
Chamaeleo gracilis	I	10	I	L	D	AL	0–1600	WE
Chamaeleo laevigatus	I	12	I	L	D	AL	1000–1500	CE
Rhampholeon boulengeri	U	2, 16	I	FI, FE	D	L, AL	1400–2000	CE
Scincidae								
Afroablepharus wahlbergii	R	9, 12	I	A,F,L	D	L,T	0–2200	CS
Eumecia anchietae	U	1,3	I	L, F	D	T	—	EA
Feylinia currori	S	2	I	FE	?	B	—	MA
Lepidothyris aff. *fernandi*	R	2	I	FE, FI		L, T	600–2100	CE
Trachylepis maculilabris	R	7	I	A, FE	D	L, T	0–2300	SSA
Trachylepis megalura	R	6,7	I	A, FE	D	L, T	1500–3000	CS
Trachylepis quinquetaeniata	C	13	I	L	D	T	200–1600	NA
Trachylepis striata	C	1,5	I	A, FE, F	D	L, T	0–2300	MA
Lacertidae								
Adolfus africanus	I	2	I	FI, FE	D	A, L	580–1200	CE
Adolfus jacksoni	C	1,5	I	FE, A, F	D	T, L	450–3000	CE
Cordylidae								
Chamaesaura anguina	R	14	I	L	D	T	1200–3000	MA
Varanidae								
Varanus niloticus	R	9	M,Ga,F, A,B,I	A, F, L	D	T	0–1600	SSA
Serpentes, Typhlopidae								
Typhlops angolensis	R	7	I	A, FE	N	B	—	CE
Typhlops lineolatus	U	2,5	I	F, FE	N	B		MA
Colubridae								
Crotaphopeltis hotamboeia	R	14	A	FE, A	N	T, Aq	0–2500	CE
Dasypeltis atra	U	2,14	B	FI, FL,L	N	T, A	1000–2800	CE
Dasypeltis scabra	U	7	B	FI, FL, L, F	N	T, A	0–2600	SSA
Dispholidus typus	R		A,Ro,B,E	FE, L, F	D	A, AL, AH	0–2200	SSA
Hapsidophrys lineatus	I	2,14	A	FE, FI	DN?	A	700–1800	WE
Lamprophis fuliginosus	C		Ro	A, F	N	T	0–2400	WE
Lycophidion capense	R	7	E,S	L, A	N	T	0–2400	CE
Lycophidion depressirostre	R	7	E,S	L	N	T	—	EA
Lycophidion ornatum	I	2	E	FI, FE	N	T	700–2700	CE
Mehelya capensis	R	14	E,S	FE, F, L	N	T	0–2000	
Natriciteres olivacea	R	4	A,F	FE, A	DN	T, Aq	0–2200	WE
Philothamnus battersbyi	U	1,14	A,F	F, W, L	D	AL	1300–1800	EA
Philothamnus carinatus	R	7	A	FI, FE	DN?	A	0–2300	WE
Philothamnus heterolepidotus	R	15	A	L	D	A	600–2000	WE
Philothamnus hoplogaster	R	14, 10	A,F	L, W	D	A	0–1800	OS
Philothamnus nitidus	R	15, 14	A	FE, FL	D	A	medium	CE
Psammophis mossambicus	I	14,1	S,E,A,B,Ro	L, F, A	D	T	0–2500	OS
Psammophis phillipsi	I	2	M,E,A,B	FE	D	A	medium	WE
Psammophis rukwae	R	7,8	E,S	L, F, A	D	T	medium	WE
Thrasops aethiopissa	U	2	A	FI, FE	DN?	A	medium	EA

Taxon	Abun[a]	Loc[b]	Diet[c]	Hab[d]	Act[e]	Micro[f]	Alt[g]	Distr.[h]
Thrasops jacksonii	U	2,14	M,E,B,A	FE, FI, A	DN	A	600–2400	CE
Toxicodryas blandingii	R	14	B,E,A,M	FE, FI	DN	A	700–2200	WE
Toxicodryas pulverulenta	R	7	Ro,E	FI, FE	N	A	medium	WE
Atractaspididae								
Polemon christyi	R	14	E	FE, FI, A	N?	B	600–1700	CE
Elapidae								
Dendroaspis jamesoni	U	14,2	Ro,B	FE, FI, A	N	A, T	600–2200	CE
Elapsoidea loveridgei	I	14,2	S,E,A,Ro	FE, L, F	N	T	600–2200	CE
Naja melanoleuca	C	14,11	A,F,S,E,M,B	FE, FI	DN	T	0–2500	SSA
Pseudohaje goldii	I	14	A,F	FI	N	A	600–1700	WE
Viperidae								
Causus lichtensteini	U	14,5	A	FI, FE	DN	T	500–2100	WE
Causus resimus	R	7	A	FE, L, F	DN	T	0–1800	WE
Atheris hispida	U	2,14	Ga,A,Ro	FE, W	N	A	900–2400	CE
Atheris squamigera	U	2,4,14,13,7	E,S,A,M	FI, FE	N	A	700–1700	WE
Bitis nasicornis	U	4,3,14	M	FI, FE,	N	T, AL	600–2400	CE
Bitis gabonica	I	14	M	FE, L	N	T	0–2100	CE

Remarks:

a - **Abun**dance, based on the number of records: C = very common; U = common, often sighted within the study and many vouchers collected; I = rare, only seen once or twice, only single vouchers; R = rare, only from literature or single vouchers; E= proposed occurrence.

b - **Loc**alities of vouchers, literature records and sightings: 1= Buyangu Village; 2= Buyangu forest; 3= Salazar Circuit; 4= Isiukhu River; 5= Udo´s Campside; 6= Liranda Hill; 7=Kaimosi; 8= reported by Spawls *et al.* 2002; 9= reported by Loveridge; 10= Nandis; 11= Malava; 12= vicinity of Kakamega Forest; 13 = Buyangu clearing; 14= Kakamega Forest in general; 15= Yala River; 16= Kisere.

c - **Diet**, A= amphibians, I= insects, Ga= gastropods, F= fishes, E= lizards, S= snakes, B= birds, M= mammals, Ro = rodents.

d - **Hab**itats, FI= forest; FE= clearings or forest edges; A= agricultural land; F= Farmland, residential area and gardens; W= waters or shores; L= Bushland and open landscape.

e - **Act**ivity, D = day active; N = night active; DN = diurnal.

f - **Micro**habitat, Aq= aquatic; B= burrowing; L= leaf litter; T= terrestrial; A= arboricol; AL= arboricol in low vegetation; AH= arboricol in trees; AP= anthropophilous.

g - **Alt**itude in metres.

h - **Distr**ibution, East to west distribution in Africa: key references: Pitman (1974), Spawls *et al.* (2002), Broadley & Howell (1991), Uetz (2002) and Chippaux (2001): CE= central to eastern Africa; CS= central to southern Africa; EA= East Africa; K= Kenya; MA= middle of Africa; NA= northern Africa; NEA= north-eastern Africa; OS= East- to South Africa; SSA= Sub-Saharan Africa; WE= West- to East Africa.

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A new *Meligethes* of the *M. pubescens* species-group from South Africa (Coleoptera, Nitidulidae, Meligethinae)

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Abstract. A new South African species (from Western Cape Province) of the recently revised *Meligethes pubescens* species-group is described as *M. colonnellii* n. sp., an updated key to the identification of the known species of the group is provided, and new data are added on the geographic distribution of the recently described *M. hermanniae* Audisio, Kirk-Spriggs & Kirejtshuk.

Keywords. Coleoptera, Nitidulidae, *Meligethes*, new species, South Africa, *Hermannia*, Sterculiaceae.

1. INTRODUCTION

Recent years have seen the description of a number of new taxa within the *Meligethes pubescens* species-group from Southern Africa (Spornraft & Audisio 1995; Kirejtshuk 1996; Audisio et al. 1998), and a revision of the group was recently published (Audisio et al. 1998).

This paper mainly deals with the description of a new South African species more closely related to *Meligethes confertus* Reitter, 1872, and to *M. aurivestis* Audisio, Kirk-Spriggs & Kirejtshuk, 1998, and includes an updated key to the identification of the known species of the group; both form part of a coming revision of the Southern African species of the subfamily Meligethinae as a whole (P. Audisio, in preparation).

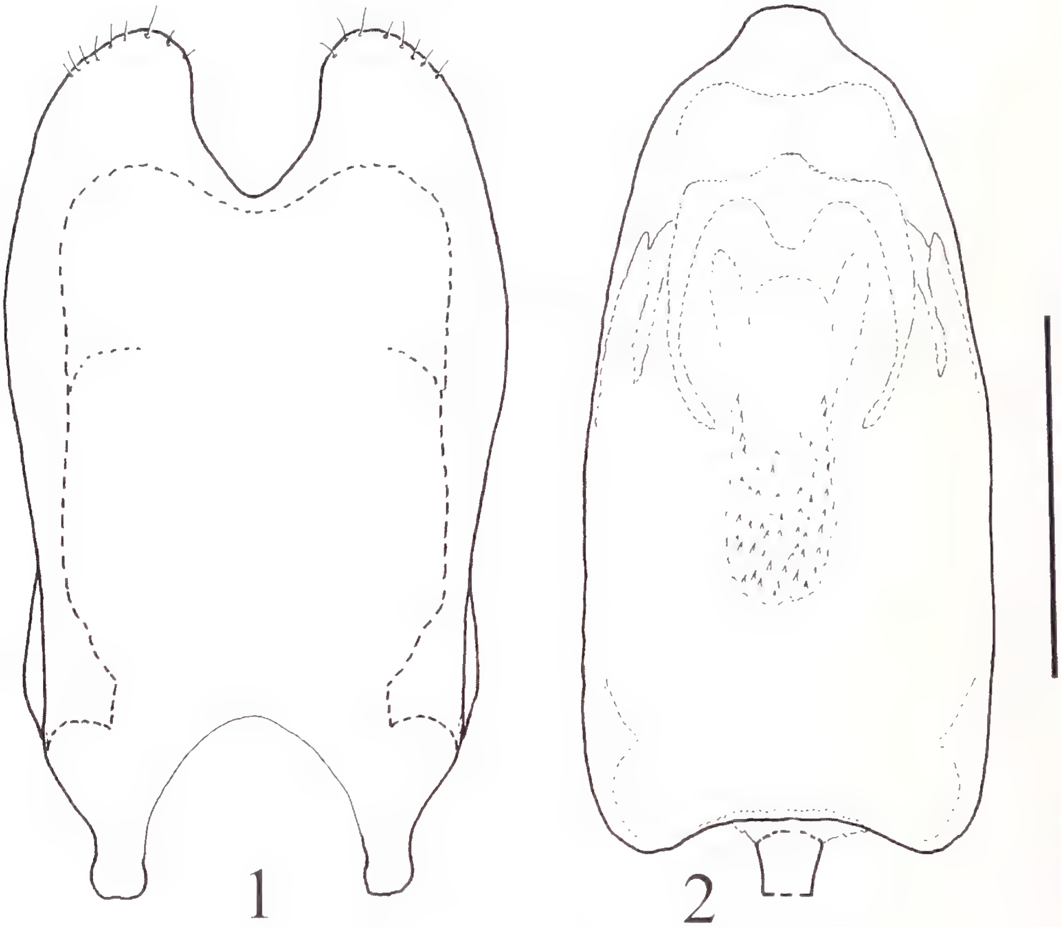
2. MATERIALS

The new species described herein was collected during two recent fieldtrips to South Africa (April–May, and October, 2005) organised by the Dept. of Animal and Human Biology of the Rome University "La Sapienza"; the studied material is mostly preserved in P.Audisio's collection, Rome (CAR), in the Albany Museum, Grahamstown (AMG) and in the Transvaal Museum, Pretoria (TMSA). Other comparative material has been borrowed for study from several South African and Namibian institutions, including the National Collection of Insects, Plant Protection Institute, Pretoria (SANC), the South African Museum, Cape Town (SAMC), the National Museum, Bloemfontein (NMBS), the Department of Entomology and Nematology, University of Stellenbosch (USSA), and the National Museum of Namibia, Windhoek (NMNW); much other (mostly unnamed) material, and the type material of all previously described species have kindly been made available for study by various European institutions, such as the Natural History Museum, London (BMNH), the Muséum National d'Histoire Naturelle, Paris (MHNP), the Zoological Museum of the University, Lund (MZLU), the Museum für Naturkunde, Humboldt University, Berlin (ZMHB), the Museum Alexander Koenig, Bonn (MAKB), the Zoological Museum of the Russian Academy of Sciences, St. Petersburg (ZMAS), the Zoologischen Staatsammlung München (ZSSM) and the Museo Civico di Zoologia, Rome (MCZR).

3. DESCRIPTION OF THE NEW SPECIES

***Meligethes colonnellii* n. sp.** (Figs 1–3)

Diagnosis. Medium-sized (length 2.8–2.9 mm), black species with orange brown legs and antennae (outer edges of all tibiae, and antennal scapes and clubs, slightly darker), with tarsal claws strongly toothed. In general appearance (Fig. 3) similar to *M. aurivestis* Audisio, Kirk-Spriggs & Kirejtshuk, 1998 (Audisio et al. 1998), but slightly narrower and less convex, without distinct metallic coppery reflections on pronotum and elytra, with finer and shorter silvery-golden dorsal pubescence, and with amply distinct male genitalia. *M. confertus* Reitter, 1872, recently re-described by Spornraft & Kirejtshuk (1993) and by Audisio et al. (1998), shows less developed elytral transverse strigosity, wider and more convex body shape, and again amply distinct male genitalia. *M. translatus* Grouvelle, 1913 (Reitter 1872; Grouvelle 1913), recently re-described by Spornraft & Kirejtshuk (1993) and by Audisio et al. (1998), shows less developed elytral trans-



Figs 1–2. Tegmen and aedeagus (dorsal aspect) of *Meligethes colonnellii* n.sp. (male holotype from Western Cape Province, 20 km S Oudtshoorn). Scale bar = 0.20 mm.

verse strigosity, longer golden pubescence, and again amply distinct male genitalia. *M. pubescens* Reitter, 1872 eventually shows strongly modified posterior tibiae in males, much less developed elytral transverse strigosity, and different male genitalia.

Description. Male. Length 2.76 mm; breadth (at widest point of elytra) 1.30 mm. Moderately elongate, oval, convex (Fig. 3); black, with moderately developed silver-golden pubescence. Legs orange brown, except for dorsal outer edges of tibiae, which are slightly darker, nut-brown. Antennae orange brown, with scape and club slightly darker.

Head with dorsal punctures as large as eye facets, rather strongly impressed, separated by less than one diameter, surface between them smooth; front margin of clypeus completely and very distinctly bordered, widely and shallowly emarginate with obtusely rounded side angles. Fronto-geneal grooves very distinct and complete. Antennae of normal size (Fig. 3), third antennal segment slender, as long as second one; antennal club medium-sized.

Pronotum 1.54 times as wide as long (Fig. 3), broadest at posterior third, narrower anteriorly; sides very narrowly bordered, not explanate; posterior angles obtuse but distinct. Posterior base not sinuate on either side of scutellum; punctures as on head, surface between them smooth and shining.

Scutellum medium-sized, finely and sparsely punctate in posterior half; surface showing a faint trace of microscopic reticulation. Elytra 1.08 times as long as wide, broadest at basal second fifth, scarcely wider than pronotum (1.07 times); shoulders feebly raised, humeral striae almost absent; elytral punctures as on head and pronotum, but slightly longer and closer, each joined to its lateral neighbours by rather strongly raised aciculation, so giving rise to a markedly distinct transrugosity, surface between them smooth.

Ventral surface black, with fine short pubescence. Prosternal antennal furrows strongly marked. Prosternal process rather long and narrow in the middle (here scarcely as wide as antennal club), with much wider and flatly rounded

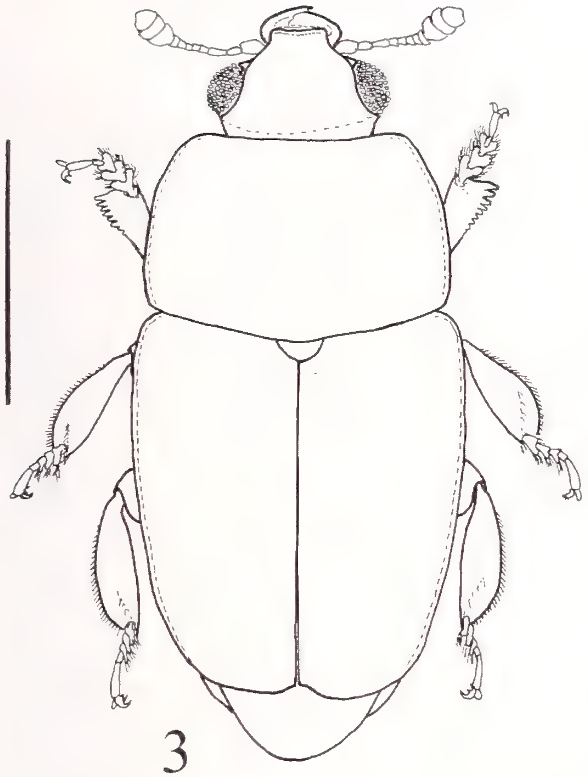


Fig. 3. Habitus (dorsal aspect) of *Meligethes colonnellii* n.sp. (male holotype from Western Cape Province, 20 km S Oudtshoorn). Scale bar = 1 mm.

apex, 1.4 times as wide as antennal club; punctures nearly as on head; surface smooth and shining. Mesosternum with hind edge straight. Metasternum rather flat (punctures and the spaces between as on head and pronotum), with a couple of small and barely distinct tubercles at its anterior two-fifths, and with a shallow longitudinal impression on its posterior two-thirds, slightly widened posteriorly. The caudal marginal line of the hind coxal cavity follows closely its posterior edge, turning back just before its outer end. Last visible abdominal sternite with its hind edge slightly and widely curving forward medially, here with a flattened, scarcely raised, but markedly shining tubercle.

Anterior tibiae (Fig. 3) shaped nearly as in *M. translatus* (Fig. 10 in Audisio et al. 1998), with their outer edges finely crenulate from basal third, then with a subapical group of 4–5 progressively larger and slightly sharper teeth, separated by one smaller tooth from the narrow subtarsal plate, but the distal teeth are of reduced size and less sharp, if compared with those of *M. translatus*, *M. aurivestis*, and *M. confertus*; anterior tarsi as wide as antennal club; intermediate and posterior tibiae with their inner edges narrowly bordered; posterior tibiae relatively narrow, their inner edges not sinuate (Fig. 3); all tarsal claws strongly toothed.

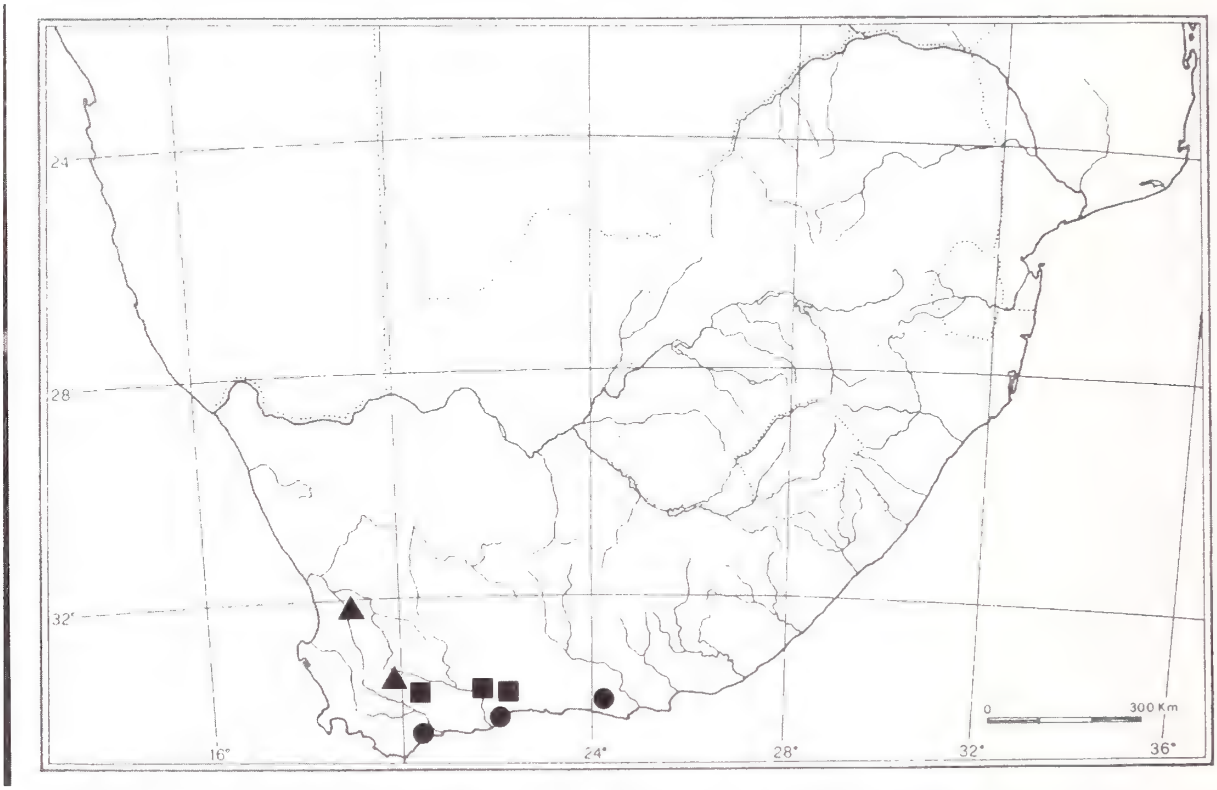
Genitalia. Tegmen (Fig. 1) with apex of paramera obtusely rounded, scarcely pubescent, and with median excision relatively small, U-shaped; aedeagus elongate (Fig. 2), strongly narrowed from distal sixth, with narrowly truncate apex.

Female. Metasternum rather flat (punctures as in male holotype), without tubercles at its anterior two-fifths, and without longitudinal impression on its posterior two-thirds. Ovipositor shaped as in *M. confertus* Reitter and *M. translatus* Grouvelle (Fig 46 in Audisio *et al.*, 1998), moderately sclerotized.

Type material:- Holotype, ♂, Republic of South Africa: Western Cape Province, Little Karoo, 20 Km S Oudtshoorn (R328), road between Oudtshoorn and the Robinson Pass, 400 m, 33°.49'.55"S, 22°.07'.13"E, 6.v.2005, P. Audisio leg., on *Asparagus* sp. (Liliaceae) (AMG). Paratypes, 1 ♂, 1 female; South Africa: Western Cape, Swartberg Mts, Seweweekspoort, NW Calitzdorp, 700 m, 33°.25'.16"S, 21°.23'.50"E, 14.x.2005, P. Audisio, M. Biondi & A. De Biase leg., by sweeping on riverine vegetation, 1 ♂ (CAR); Western Cape Province, Langeberg Mts, road between Ashton and Montagu, Kogmanskloof, 180 m, 33°.49'.26"S, 20°.05'.25"E, 9.x.2005, P. Audisio, M. Biondi & A. De Biase leg., by sweeping on riverine vegetation, 1 female (CAR).

Comparative notes. *M. colonnellii* n. sp. is rather closely related to *M. aurivestis* Audisio, Kirk-Spriggs & Kirejtshuk, *M. confertus* Reitter and *M. translatus* Grouvelle, from which it differs by the characters given in the diagnosis and in the following keys. Easily recognizable also from other related members of the genus, such as *M. pubescens* Reitter and *M. hermanniae* Audisio, Kirk-Spriggs & Kirejtshuk, by the not sinuate inner edges of the posterior tibiae, and the strongly differing male genitalia.

Biological notes. The type specimen of the new species was collected in late Autumn (May) by sweeping in disturbed fynbos from flowers of an unidentified *Asparagus* sp. (Liliaceae) with white flowers, which is clearly not its true larval host-plant. The above listed paratypes have been both collected by sweeping on riverine herbaceous vegetation. Larvae very likely develop in late Summer/Autumn on certain hygrophilous species of the genus *Hermannia* (Sterculiaceae; Verdoorn 1980; Arnold & De Wet 1993), given that all its closely related species are associated with members of this botanical genus (Audisio et al. 1998). The holotype and the two paratypes were collected in company of several specimens of the common and widespread *Meligethes pubescens* Reitter.



Figs 4. Known geographic distribution of *Meligethes colonnellii* n.sp. (squares), *M. hermanniae* Audisio, Kirk-Spriggs & Kirejtshuk (circles), and of *M. aurivestis* Audisio, Kirk-Spriggs & Kirejtshuk (triangles).

Geographic distribution. So far only known from the above mentioned localities in the Western Cape Province (Fig. 4); this species is probably more widely distributed throughout the mountain areas bordering the Little Karoo and the south eastern edge of the Great Karoo.

Etymology. This species is so named from our colleague and friend Enzo Colonnelli (Rome), renowned specialist in Curculionidae Ceutorhynchinae, in whose company the first known specimen of the new species was collected by the senior author.

4. ADDITIONAL NOTES

Meligethes hermanniae Audisio, Kirk-Spriggs & Kirejtshuk, 1998

Examined material: South Africa, Eastern Cape Province, 10 km W Kareedouw, 600 m, 33°.55'.41"S, 24°.14'.32"E, 5.v.2005, E. Colonnelli leg., on flowering bush of *Protea* sp. (Proteaceae), 1 ♂ (CAR).

This species, at larval stage associated with *Hermannia salviifolia* L. fil. (Sterculiaceae), was known so far only from two coastal localities of the eastern areas of the Western Cape Province (Audisio et al. 1998; fig. 4). The above reported new locality significatively extends eastwards and inwards the geographic range of this species. The mentioned male specimen from Kareedouw area is peculiarly large, reaching 3.0 mm in length.

5. UPDATED KEY TO THE SPECIES OF THE *MELIGETHES PUBESCENS* SPECIES-GROUP

Refer to Figs 1–71 of the Audisio et al. (1998) revision (indicated in *italic*) and to Figs 1–5 of the present paper (indicated in **bold**).

1 (2) Fronto-geneal and periocular grooves on head absent (*as in fig. 53*) 3

2 (1) Fronto-geneal and periocular grooves on head distinct (*as in fig. 54*) 9

3 (4) Tarsal claws with a well-formed, large and sharp tooth at base (*as in Fig. 55*). Male genitalia with aedeagus peculiarly long and narrow (*Figs 30–32*); ovipositor peculiarly small and unsclerotized (*Fig. 51*). Anterior tibiae with minute and irregular teeth on their distal outer edges (*Fig. 16*). Eastern Cape Province, Natal, southern Mpumalanga (= Eastern Transvaal) (*Fig. 63*) . . . . **15. *marshalli*** Grouvelle

4 (3) Tarsal claws with a virtually undeveloped tooth at base (*as in fig. 57*), or with a blunt tooth at base (*as in fig. 56*). Male genitalia with aedeagus considerably less elongate (*Figs 43–44, 68–71*); ovipositor larger (*Fig. 50*), or at least more sclerotized (*Fig. 52*) 5

5 (8) Tarsal claws with a blunt tooth at base (*as in fig. 56*). Anterior tibiae with a series of 5/10 sharp teeth placed in their distal half or two-thirds, an intermediate one and the penultimate usually being the largest (*as in fig. 13*). Body usually brown to blackish, with yellowish to orange legs and antennae, sparse and more or less conspicuous silvery, or golden pubescence, and elytra paler, or with a large reddish discal spot 6

6 (7) Dorsal and ventral pubescence usually silvery, more conspicuous, each hair being moderately long, but of unusually large diameter. Male genitalia smaller, shaped as in *figs 70–71*. Ovipositor as in the following species (*Fig. 50*). Northern and eastern Namibia, Botswana, northern parts of South Africa (*Fig. 64*) . . . . **12. *rufofuscus*** Audisio, Kirk-Spriggs & Kirejtshuk

7 (6) Dorsal and ventral pubescence golden, less conspicuous, each hair being moderately long and fine. Male genitalia larger, shaped as in *figs 68–69*. Ovipositor as in *fig. 50*. Central and southern Namibia, Namaqualand (*Fig. 64*) . . . . **13. *eremita*** Audisio, Kirk-Spriggs & Kirejtshuk

8 (5) Tarsal claws lacking a distinct tooth at base (*as in fig. 57*). Anterior tibiae with a series of small, irregular and usually blunt teeth on their distal outer edges (*Fig. 17*). Body unicolorous blackish-brown, with legs and antennae brown to blackish. Male genitalia as in *figs 43–44*. Ovipositor as in *fig. 52*. NE Eastern Cape Province, southern Kwa Zulu-Natal (*Fig. 61*) . . . . **14. *argentarius*** Audisio, Kirk-Spriggs & Kirejtshuk

9 (10) Tarsal claws simple, lacking a distinct tooth at base (*as in Fig. 57*) 11

10 (9) Tarsal claws with a well-formed, large and sharp tooth at base (*as in Fig. 55*) 19

11 (12) Last segment of the antennal club peculiarly large (*Fig. 21*). Body peculiarly large, short and convex (*Fig. 65*). Anterior tibiae as in *fig. 18*. Male genitalia as in *figs 66–67*. Northern Transvaal (*Fig. 62*). ....**11. *massivus*** Audisio, Kirk-Spriggs & Kirejtshuk

12 (11) Last segment of the antennal club much smaller, and normally shaped (*Figs 1–5*) 13

13 (14) Dorsal pubescence golden or silvery, scarcely long and dense, never obscuring upper surface. Outer edges of anterior tibiae with a series of 7/12 sharp and usually irregular teeth, never regularly increasing in size from the first to the penultimate (*Figs 14–15*). (The *M. fuerschi*-complex) 15

14 (13) Dorsal pubescence golden or silvery, peculiarly long and dense, partially obscuring upper surface (in unrubbed specimens). Outer edges of anterior tibiae with a series of 7/10 more or less sharp teeth placed in their distal three-fifths, usually slightly and regularly increasing in size from the first to the penultimate, which as a rule, is the largest (*Figs 11–12*). (The *M. plumbeus*-complex) 17

15 (16) Elytra strongly transversely strigose. Male genitalia with a very small and shallow distal excision on tegmen (*Fig. 26*) and moderately pointed aedeagus (*Fig. 27*). Ovipositor slightly more pointed (*Fig. 49*). Southern parts of the Western Cape Province, eastern Free State (*Fig. 62*) . . . .**10. *pecten*** Audisio, Kirk-Spriggs & Kirejtshuk

16 (15) Elytra less strongly transversely strigose. Male genitalia with much deeper and narrow distal excision on tegmen (*Fig. 28*), and subtruncate aedeagal apex (*Fig. 29*). Ovipositor slightly less pointed (*Fig. 48*). Eastern parts of

the Eastern Cape Province and of the Free State, Kwa Zulu-Natal, and Mpumalanga (*Fig. 62*). . . . . **9. *fuerschi*** Spornraft & Audisio

17 (18) Metasternum flat, not impressed in both sexes. Male genitalia much shorter (*Figs 35–36*). Ovipositor as in *fig. 47*. Western parts of the Western Cape Province (*Fig. 59*) . . . . **8. *plumbeus*** Reitter

18 (17) Metasternum shallowly impressed in males. Male genitalia much longer and differently shaped (*Figs 33–34*). Ovipositor as in *M. plumbeus* (*fig. 47*). Western parts of the Western Cape Province, southern Namibia (*Fig. 61*) . . . . **7. *namakwaensis*** Audisio, Kirk-Spriggs & Kirejtshuk

19 (20) Inner edges of posterior tibiae markedly sinuate at distal third in both sexes (*as in fig. 19*). (The *M. pubescens*-complex) 21

20 (19) Inner edges of posterior tibiae not sinuate at distal third in both sexes (*as in fig. 20* **and in fig. 3**). (The *M. confertus*-complex) 23

21 (22) Male genitalia much longer and larger, with median distal excision of tegmen more rounded basally (*Figs 24–25*). Body on average larger (length: 2.3–3.0 mm). Eastern coastal and subcoastal areas of the Western Cape Province and of the western portion of the Eastern Cape Province (**Fig. 4**) . . . . **2. *hermanniae*** Audisio, Kirk-Spriggs & Kirejtshuk

22 (21) Male genitalia much shorter and smaller, with median distal excision of tegmen V-shaped basally (*Figs 22–23*). Body on average smaller (length: 2.2–2.8 mm). Southern parts of the Western Cape Province and SW parts of the Eastern Cape Province (*Fig. 59*) . . . . **1. *pubescens*** Reitter

23 (24) Pronotum more distinctly narrower than elytra (*Fig. 4*); pronotum and elytra partially covered by usually golden pubescence. Elytra without, or with only a faint trace of transverse strigosity. Male genitalia with distal apex of tegmen with deep and wide V-shaped excision (*Figs 37–38*). Subdesertic inner parts of the Western Cape Province and extreme West of the Northern Cape Province (*Fig. 60*) . . . . **3. *translatus*** Grouvelle

24 (23) Pronotum nearly as wide as elytra (*as in fig. 3* **and 3**); pronotum and elytra partially covered by usually silvery, silvery-golden, or olivaceous pubescence. Elytra with distinct traces of, or with strong, transverse strigosity. Male genitalia differently shaped (*Figs 39–42;* **Figs 1–2**) 25

25 (26) Usually only with trace of elytral transverse strigosity. Male genitalia differently shaped, with distally widely truncate median lobe of aedeagus, but without distally subtruncate tegmen (*Figs 39–40*). Body lacking a faint coppery reflection. Southern parts of the Western Cape Province and SW parts of the Eastern Cape Province (*Fig. 60*) . . . . **4. *confertus*** Reitter

26 (25) Elytra with strong transverse strigosity. Male genitalia with very peculiarly shaped and distally truncate tegmen (*Fig. 41*), or with median lobe of the aedeagus much more narrowly pointed at the apex (**Fig. 2**) 27

27 (28) Body with a faint coppery reflection, especially dorsally. Dorsal pubescence silvery-olivaceous, longer and more developed. Male genitalia with much more widely truncate apex of the median lobe of aedeagus, combined with a subtruncate apex of tegmen, with short U-shaped median excision of the latter (*Figs 41–42*). Montane areas of the SW Western Cape Province (**Fig. 4**) . . . . **5. *aurivestis*** Audisio, Kirk-Spriggs & Kirejtshuk

28 (27) Body without coppery reflection. Dorsal pubescence silvery-golden, finer and less developed. Male genitalia with much more narrowly truncate apex of the median lobe of aedeagus, combined with roundly obtuse apex of paramera, with short U-shaped median excision of tegmen (**Figs 1–2**). Montane areas of the SE Western Cape Province (**Fig. 4**) . . . . **6. *colonnellii* n.sp.**

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(2003): Band 1: Allgemeiner Teil; Fledermäuse (Chiroptera). 688 S., 320 Farbphotos, 49 SW-Photos, 186 Diagramme & Zeichnungen, 46 Verbreitungskarten, 55 Tabellen. Preis 49,90 €
(2005): Band 2: Insektenfresser (Insectivora), Hasentiere (Lagomorpha), Nagetiere (Rodentia), Raubtiere (Carnivora), Paarhufer (Artiodactyla). 704 S., 193 Farbphotos, 2 SW-Photos, 172 Diagramme & Zeichnungen, 47 Verbreitungskarten, 138 Tabellen. 49,90 €. Eugen Ulmer Verlag, Stuttgart.

Mit dem Erscheinen des 2. Bandes so relativ kurz nach dem des 1. liegt dieses eindrucksvolle Werk mit zusammen weit mehr als 1000 Seiten nun komplett vor. Grundlage seiner Veröffentlichung ist das langjährige und aus öffentlichen Mitteln geförderte Forschungsprojekt „Wild lebende Säugetiere in Baden-Württemberg". Außer von den beiden Herausgebern enthalten die beiden Bände Textbeiträge von jeweils 20 weiteren Autoren. Entscheidend für das Projekt und die Fülle der darin präsentierten Daten war sicherlich auch die ehrenamtliche Mitarbeit von über 1000 weiteren Personen, die Beobachtungsdaten und Hinweise zum Vorkommen von Säugetieren in Baden-Württemberg beigetragen haben.

Den ersten Teil des 1. Bandes mit nahezu 300 Seiten bildet der Allgemeine Teil mit u.a. den folgenden Kapiteln: Säugetiere (Kennzeichen, Verbreitung und Vielfalt); Zur Geschichte der Erforschung der Säugetierfauna (allgemein und regional in Württemberg und Baden); Naturräume in Baden-Württemberg [im folgenden: B-W]; Methoden der Datenerhebung und Datenverarbeitung; Gewölleanalyse; Die Säugetiere im Quartär von B-W; Einwanderung, Einbürgerung und (Wieder-) Ansiedlung von Säugetieren; Jagd; Domestizierte Säugetiere in B-W; Zoonosen wildlebender Säugetiere in B-W; Gefährdungsursachen; Schutzmöglichkeiten; Rote Liste der gefährdeten Säugetiere in B-W. Er spannt damit einen wirklich weiten thematischen Bogen. Den anschließenden Speziellen Teil von nahezu 400 Seiten Umfang leitet ein allgemeines Kapitel über Säugetiere zu „Klassifikation, taxonomische Merkmale, Maße, Fachbezeichnungen u.a." ein, gefolgt von einer Einführung in die Ordnung Chiroptera, einem Überblick über die heimischen Fledermäuse und einem Bestimmungsschlüssel der mitteleuropäischen Arten nach äußeren Kennzeichen und Zahnmerkmalen. Ausführliche monographische Abhandlungen zu 22 in B-W vorkommenden Fledermausarten schließen sich an. Die Artkapitel sind jeweils nach einem weitgehend einheitlichen Schema gegliedert und behandeln folgende Themen: Namensgebung (Taxonomie und Geschichte des deutschen Trivialnamens); Beschreibung (äußere Merkmale, Maße und Gewicht, Schädel und Gebiss [bei einander ähnlichen Arten wird ausführlich auf Unterscheidungsmerkmale eingegangen]); Verbreitung (Artareal insgesamt, in Deutschland und speziell in B-W); Lebensraum; Lebensweise (Sommerquartiere, Nahrungsökologie, Echoortung, Fortpflanzung, Wanderungen, Winterquartiere und Winterschlaf, Populationsdynamik); Artenschutz. Am Beginn des 2. Bandes wird das Projekt, das Grundlage der vorliegenden Veröffentlichung war, noch einmal kurz vorgestellt, gefolgt von einer erneuten kleinen Einführung in Datenerhebung und Datendarstellung sowie zu den für Säugetieren spezifischen Maßangaben. Daran schließt sich auf mehr als 600 Seiten die Darstellung der übrigen in B-W vorkommenden Säugetierarten aus den Ordnungen der Insectivora (11 Arten) (der aktuelle Erkenntnisstand, wonach die Zusammenfassung der Igel mit Spitzmäusen und Maulwürfen in einer gemeinsamen Ordnung keine natürliche Verwandtschaftsgruppe darstellt, wurde hier noch nicht berücksichtigt), Lagomorpha (3 Arten), Rodentia (21 Arten), Carnivora (14 Arten) und Artiodactyla (7 Arten) an. Auch in diesem Band gibt es zu allen Ordnungen jeweils kürzere allgemeine Einführungskapitel (bei den Artiodactyla auch zu den Unterordnungen der Nichtwiederkäuer und der Wiederkäuer), ebenso zu den jeweiligen Familien (bei den Rodentia auch zu Unterfamilien). Der Aufbau der einzelnen Artkapitel folgt einem ähnlichen Schema wie in Band 1, es fehlen aber durchgehend die Ausführungen zur Namensgeschichte. Besonders eingehend wird die Lebensweise der einzelnen Arten mit Ausführungen zu Verhalten, Aktivität, Fortbewegung, Aktionsraum, Sinnen, Kommunikation, Lautäußerungen, Ernährung, Fortpflanzung, Jugendentwicklung, Populationsdynamik, natürlichen Feinden, Parasiten und Krankheiten sowie – wo relevant – auch zur Bejagung und deren Auswirkungen dargestellt.

Alle Beiträge sind in ihrer Darstellung allgemeiner Zusammenhänge und der zu den einzelnen Arten präsentierten Fakten fachlich fundiert und bereiten für den betroffenen geographischen Raum eine große Fülle interessanter Einzeldaten auf; diese wiederum werden dann in sinnvoller Weise in einen größeren Zusammenhang gestellt. Auch in ihrer Ausstattung, ihrem Druck und der Zahl und Qualität der Abbildungen werden diese beiden Bände hohen Ansprüchen gerecht. Bei einem so umfangreichen Werk, an dem viele Autoren mitgewirkt haben, ist es fast unvermeidlich, dass sich hier und da Uneinheitlichkeiten der Darstellung oder auch kleinere redaktionelle Fehler einschleichen. Um nur ein Beispiel zu nennen: In Band 2 sind in Tabelle 60 (S. 357) für die Felidae rezent 11 Gattungen und 36 Arten aufgeführt, der anschließende Text auf S. 358 nennt aber 18 Gattungen und 35 Arten. Als wenig nutzerfreundlich empfindet es der Rezensent, dass das vollständige Literaturverzeichnis am Ende des 2. Bandes nach den einzelnen darin behandelten Säugerordnungen unterteilt ist. So sucht man erst einmal nach der Seite, auf der die Literaturzitate für die jeweiligen Ordnungen beginnen und kann erst dann gezielt alphabetisch nach dem speziellen Zitat suchen, an dem man interessiert ist. Im 1. Band ist dies besser gelöst; dort folgen dem Allgemeinen Teil und dem Speziellen Teil die jeweiligen Literaturverzeichnisse.

Von solchen wirklich geringfügigen Kritikpunkten abgesehen gebührt den Förderern des Projekts, aus dem diese Veröffentlichung hervorgegangen ist, Dank und allen anderen daran beteiligten Personen, besonders natürlich den beiden Herausgebern, ausdrückliche Anerkennung für diese Leistung. Diese beiden Bände gehören ohne Einschränkung in jede größere öffentliche Bibliothek, die von ernsthaft an unseren heimischen Säugetieren interessierten Personen genutzt wird. Wer beruflich mit diesen Tieren arbeitet, sollte sich dieses Werk auf jeden Fall anschaffen. Wenn man einmal vom viel umfangreicheren „Handbuch der Säugetiere Europas" absieht (das primär für einen anderen Nutzerkreis gedacht ist), gibt es aktuell auf dem deutschsprachigen Buchmarkt keine auch nur annähernd in Qualität und Informationsfülle vergleichbare Veröffentlichung zur Biologie (im weitesten Sinne) der heimischen Säuger – und es besteht wohl auch wenig Aussicht, dass auf absehbare Zeit eine solche erscheinen wird. Angesichts der bedauernswerten Entwicklung, dass die organismische Biologie im Unterricht an weiterführenden Schulen und im Grundstudium der Biologie immer weiter zurückgedrängt wird, kann man nur hoffen, dass diese beiden Bände in diesen Schulen und in den betreffenden Universitätsinstituten angeschafft werden und eine möglichst intensive Nutzung erfahren.

Gustav PETERS, Zoologisches Forschungsmuseum Alexander Koenig, Bonn

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Morphological differentiation of mainland Citril Finches, *Carduelis* [*citrinella*] *citrinella* and insular Corsican (Citril) Finches, *Carduelis* [*citrinella*] *corsicanus*

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The Citril Finch is one of the few endemic bird species restricted to European mountains (VOOUS 1960; NEWTON 2003). Two allopatric forms may be distinguished. Insular Corsican (Citril) Finches, *Carduelis [citrinella] corsicanus*, live exclusively on Corsica, Sardinia and some Tuscany islands (Capraia, Elba, Gorgona) (ARCAMONE 1993; BACCETTI & MÄRKI 1997; CRAMP & PERRINS 1994; THIBAULT 1983; THIBAULT & BONACCORSI 1999; MOLTONI 1975), whereas mainland Citril Finches, *Carduelis [citrinella] citrinella*, occur at higher elevations in the mountain ranges of central and south-western Europe (Alps, Black Forest, Vosges, Jura, Massif Central, Cevennes, Pyrenees, Cantabrians and Sierras of central Spain), generally above 800 m asl. (BACCETTI & MÄRKI 1997; CRAMP & PERRINS 1994; GLUTZ VON BLOTZHEIM & BAUER 1997; HÖLZINGER 1997).

There is an ongoing debate about the taxonomic status of Citril Finches and Corsican Finches. In spite of recently detected genetic differences (mitochondrial DNA differs by 2.7 %), the authors of these studies still regard the two forms as conspecific (PASQUET & THIBAULT 1997; THIBAULT & BONACCORSI 1999). In contrast, SANGSTER (2000) assigned species status to the Corsican Finch, referring to the same genetic results. Based on his recommendations in combination with data on variations in plumage colouration (CRAMP & PERRINS 1994; PASQUET 1994) and vocalization (CHAPPUIS 1976; CRAMP & PERRINS 1994; recently confirmed by FÖRSCHLER & KALKO 2007), the Association of the European Rarities Committees (AERC) now treats the two forms as full species with their own evolutionary histories (SANGSTER et al. 2002). Furthermore the two species have been recently reclassified within the genus *Carduelis* instead of being a member of *Serinus* (ARNAIZ-VILLENA et al. 1998, 1999). Both forms are therefore members of the superspecies *Carduelis [citrinella]* (BARTHEL & HELBIG 2005; Helbig 2005). Only little data has been published on evidence for differentiation in morphological character traits between the two forms. According to the available notes on morphometry, both species do not show large geographical differences in body size (ALONSO & ARIZAGA 2006; BORRAS et al. 1998; BRANDL & BEZZEL 1989; CRAMP & PERRINS 1994; MÄRKI & BIBER 1975), with the exception that Corsican Finches seem to have generally slightly shorter wings than nominate Citril Finches (CRAMP & PERRINS 1994). Nominate birds in the Eastern Pyrenees appear to have longer wings than do nominate birds in the Alps, but evidence is weak and may be also due to variation between different measurers (BRANDL & BEZZEL 1989; BORRAS et al. 1998; MÄRKI & BIBER 1975). Adult male Citril Finches have an average population weight of 12.5 g in the Eastern Pyrenees (BORRAS et al. 1998), while adult male Corsican Finches are little bit lighter with 11.5 g in average (NICOLA BACCETTI, GILLES FAGGIO, SERGIO NISSARDI & PHILIPPE PERRET, pers. comm.).

We analysed 20 morphological character traits following the methods of LEISLER & WINKLER (1985, 1991, 2001), LEISLER et al. (1997) and KORNER-NIEVERGELT & LEISLER (2004). The following external features were measured. (1) wing length (the distance between carpal joint and tip of falltened wing); (2) tail length (from insertion of central pair of feathers to tip of longest rectrix); (3) fork of the tail (difference from longest to shortest inner rectrix); (4) wing width (the distance between carpal joint and the tip of the longest secondary); (5) primary projection (the distance between tip of 1st secondary and wing tip); (6) distal (the distance between tip of 10th primary and wing tip); (7) alula (the distance between carpal joint and tip of the longest alula); (8) notch P2i (length of notch on inner web of second primary); (9) notch P3o (length of notch on outer web of third primary); (10) Kipp Index (distance of 1st secondary to wing tip x 100/ wing length see KIPP

1959) (11) bill length (from tip to skull); (12) bill width (at the rear end of nostrils); (13) bill height (maximum depth); (14) rictal bristles (the length of the vibrisse at the bill base) (15) tarsus length (from notch of the intertarsal joint to the lower edge of the last complete scale); (16) tarsus diameter 1 (lateral maximal diameter of tarsus); (17) tarsus diameter 2 (sagittal maximal diameter of the tarsus; (18) hind toe (length of digit 1); (19) middle toe (length of digit 3); (20) hind claw (the cord from the tip to dege of the skin of nail); (21) middle claw (the chord of nail 3); (22) index of wing length/ tarsus length.

In total we measured 23 individuals of mainland Citril Finches from the Northern Alps and 13 individuals of insular Corsican Finches from Corsica and Sardinia. For our study we used only adult males to guarantee comparability. All measurements were conducted by Karl Heinz Siebenrock. Museum specimens from the following museum collections were used exclusively: Zoologische Staatssammlung München (Munich), Zoologisches Museum der Humboldt Universität (Berlin) and Naturkundemusem Rosenstein (Stuttgart).

We found significant morphological differentiation between mainland Citril Finches and insular Corsican Finches (see Table 1). Corsican Finches are generally smaller. Wings are considerably longer and more pointed (Kipp Index) in Citril Finches. Accordingly, significant variations may be also found between other wing measurements (secondary, primary projection, distal, alula, notch P2i, notch P3o). Corsican Finches have a shorter tail and their tail is less forked. Furthermore Citril Finches possess significantly broader, higher and longer bills than Corsican Finches. No significant difference was found for the length of the rictal bristles. Citril Finches have longer and stonger tarsi, a longer middle toe and longer claws. However the length of the hind toe (maybe due to measurement errors) and the ratio of wing length to tarsus length are not significantly different.

Climate is known to play an important role in geographic size variation (James 1970; Johnston & Seleander 1973). Corsican Finches appear to inhabit generally areas of warmer clime than do Citril Finches (Thibault & Bonaccorsi 1999) and may therefore have developed

Table 1. Mean values of 20 morphological traits and 2 indices of Citril and Corsican Finches. Comparisons were conducted with t-tests (parametric distributed data sets) and Mann Whitney U tests (non-parametric distributed data sets).

	Citril Finch (n=23) in mm	**Corsican Finch** (n=13) in mm	**Statistical comparison**	**Sign-Level**
Flight apparatus				
Wing length	76.4±1.5 SD	72.5±2.2 SD	t-test; t=6.569; df=34; p≤0.001	***
Tail length	53.3±1.8 SD	50.4±2.2 SD	t-test; t=4.336; df=34; p≤0.001	***
Fork of the tail	-10.0±1.1 SD	-7.2±1.1 SD	MWU; T=94; p≤0.001	***
Wing width	53.5±1.6 SD	51.0±1.6 SD	MWU; T=126.0; p≤0.001	***
Primary projection	22.6±1.2 SD	20.1±1.5 SD	t-test; t=5.319; df=34; p≤0.001	***
Distal	54.1±1.4 SD	50.3±2.1 SD	MWU; T=118.5; p≤0.001	***
Alula	56.4±1.5 SD	52.8±2.3 SD	MWU; T=119; p≤0.001	***
Notch P3o	23.1±1.4 SD	21.0±1.2 SD	t-test; t=4.692; df=33; p≤0.001	***
Notch P2i	19.8±0.8 SD	17.7±1.1 SD	MWU; T=94; p≤0.001	***
Kipp index	29.6±1.3 SD	27.8±1.9 SD	t-test; t=3.439; df=34; p=0.002	**
Feeding apparatus				
Bill length	12.2±0.6 SD	11.6±0.5 SD	MWU; T=133.0; p≤0.001	***
Bill width	5.3±0.2 SD	4.8±0.3 SD	MWU; T=115.5; p≤0.001	***
Bill height	6.2±0.3 SD	5.6±0.3 SD	t-test; t=6.432; df=34; p≤0.001	***
Rictal bristles	2.6±0.7 SD	2.4±0.7 SD	t-test; t=4.950; df=34; p=0.420	ns
Hind limb				
Tarsus length	14.4±0.6 SD	13.5±0.5 SD	t-test; t=4.653; df=34; p≤0.001	***
Tarsus diameter 1	0.88±0.08 SD	0.82±0.06 SD	t-test; t=2.278; df=34; p=0.034	*
Tarsus diameter 2	1.34±0.13 SD	1.15±0.06 SD	t-test; t=4.950; df=34; p≤0.001	***
Hind toe	6.5±0.4 SD	6.4±0.3 SD	t-test; t=0.599; df=34; p=0.553	ns
Middle toe	10.9±0.6 SD	10.2±0.6 SD	t-test; t=3.240; df=34; p=0.003	**
Hind claw	6.1±0.5 SD	5.6±0.5 SD	t-test; t=2.926; df=34; p=0.008	**
Middle claw	5.4±0.4 SD	4.7±0.4 SD	t-test; t=5.534; df=34; p≤0.001	***
Wing length/ tarsus index	5.3±0.2 SD	5.4±0.2 SD	MWU; T=267; p=0.392	ns

smaller body size and body weight. However, this supposed climatic difference is essentially not the case for a majority of Corsican Finches, living on the highest mountain slopes of Corsica, where climatic conditions are quite comparable to the Alps or Pyrenees. Furthermore, measurements conducted by BORRAS et al. (1998) revealed no clear clinal variation in size from north to south in mainland Citril Finches as expected. They propose that other factors such as habitat or diet may be of larger importance.

We suggest therefore that the morphological differentiation observed in our study may have evolved as a consequence of different habitat conditions, since Citril and Corsican Finches differ in several features of habitat choice (FÖRSCHLER & KALKO 2006b). While Citril Finches prefer semi-open conifer forests, especially pine woodland in higher mountains, Corsican Finches generally inhabit more open habitats dominated by Tree Heath, *Erica arborea*. It is highly probable that Citril Finches are adapted to forage over longer distances (longer and more pointed wings, longer tail) and probably also to perch on stronger branches and twigs of pine trees (stronger feet), whereas Corsican Finches appear to show rather adaptations to the Macchia thickets with Tree Heath or other scrub vegetation of Mediterranean islands (FÖRSCHLER & Kalko 2006b). As a consequence Corsican Finches may have developed smaller and less pointed wings and shorter tails due to the reduction of long distance migration (THIBAULT & BONACCORSI 1999), favouring more the manoeuvrability within the Mediterranean scrub vegetation. In this context, the difference in bill size might be explained by variations in feeding ecology of the two species (FÖRSCHLER & KALKO 2006a) with Citril Finches probably more adapted to larger seeds (mainly those from pines) and Corsican Finches more adapted to smaller herb seeds (e.g. Shepherd´s Purse). Further analyses may reveal how the morphological differentiation in the locally isolated populations of these two allopatric forms has evolved in relation to distinct ecological conditions and adaptation processes.

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African Coleoptera Type Specimens collected by Thomas Wagner in the collection of the ZFMK

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Abstract. The type specimens of African Coleoptera from material collected by Thomas Wagner mainly using insecticidal canopy fogging technique and housed in the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, are listed. There are 71 names recorded; of these 37 (52%) are represented by holotypes. Specific names are sorted by their respective family and both are listed alphabetically. Reference to the original description of each taxon is provided and sex and number of each type given as well as images of the name bearing primary types.

Keywords. Type specimens, canopy fogging, Coleoptera, Africa.

1. INTRODUCTION

Thomas Wagner's material at the Zoologisches Forschungsmuseum (ZFMK) house African Coleoptera mainly collected in Rwanda, Kenya and Uganda from 1993 until today by insecticidal tree fogging. Voucher specimens were computerized within phase II of the German BIOTA East Africa Project (subproject BIOTA E15: "Capacity building in biodiversity information systems for insects and plants in East Africa") which is financially supported by the German Ministry of Science and Education (BMBF) and runs until May 2007. Data capture was done with the specimen based database BIODAT. By adaptation to the ABCD schema (Access to Biological Collection Data) BIODAT became both a BIOCASE- (Biological Collection Access Service for Europe) and GBIF- (Global Biodiversity Information Infrastructure) provider. Therefore full information at the specimen level, and not only of type specimens, for selected ZFMK insect collections will be commonly available on the World Wide Web (http://www.biodat.de). In case of type specimens images of the type itself and of the original labels are provided. The present catalogue covers 370 type specimens of 71 species of which 37 are represented by holotypes.

In this publication the specific taxa of Coleoptera are grouped by families and arranged alphabetically. They are listed by species epitheta, author, year of publication, page number where species was described, original generic assignment in brackets followed by the catalogue number/s, number/s sex and kind of type specimen. All primary types are listed with the original label information, supplemented by date and place collected information. Normally 'named area' information is used. If available the exact 'gathering site' information is indicated by geographical coordinates (Latitude/Longitude). Higher ranked geographic information such as region, country and continent is added in a hierarchy. To avoid hypertrophic text length most of the secondary types are listed without original label information. If the collection, however, harbours only secondary types of a given taxon the original label information is given for the first type specimen. Images of the primary types are provided.

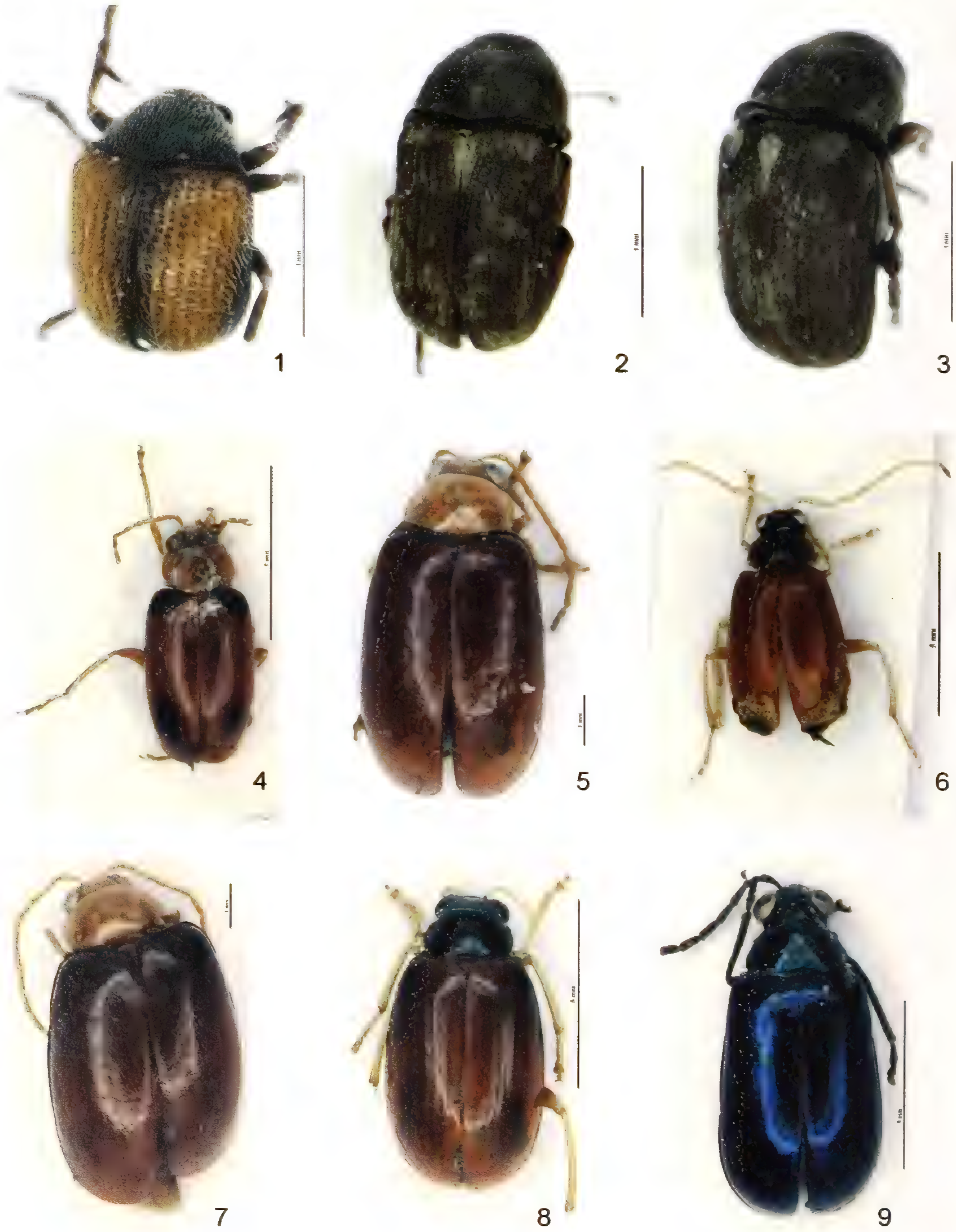
The following abbreviations were used in the lists: HT – holotype, PT – paratype, AT – "allotype" .

Coleoptera

Anthribidae

cognatus Frieser, 1997: 12 *(Mecocerus)*
COL 2006/188 **1 ♀ PT**
Rwanda, Nyakabuye - Cyamudongo X.93 - Th. Wagner leg. / C.g.7 1 / Paratype / Mecocerus cognatus sp. n. - Paratypus ♀ - det. R. Frieser 1996
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33'S, 28°59'E (gathering site: estimated value)

marginalis Frieser, 1997: 19 *(Triplodus)*
COL 2006/185 **♂ HT** **(Fig. 1)**
Rwanda, 1700 m - Cyamudongo, X.93 - Th. Wagner leg. / C.g.4 3 / Holotype / Triplodus marginalis sp. n. – Holotypus ♂ - det. R. Frieser 1996
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33'S, 28°59'E (gathering site: estimated value)



Figs 1–9. *Triplodus marginalis* Frieser, 1997 (**1**) ♂ HT, *Uncifer nubilus* Frieser, 1997 (**2**) ♂ HT, *Uncifer proprius* Frieser, 1997 (**3**) ♂ HT, *Monolepta alwineae* Wagner, 2002 (**4**) ♂ HT, *Monolepta budongoensis* Wagner, 2002 (**5**) ♂ HT, *Monolepta comoeensis* Wagner, 2000 (**6**) ♂ HT, *Monolepta congoensis* Wagner, 2002 (**7**) ♂ HT; *Monolepta constantini* Wagner, 2002 (**8**) ♂ HT, *Bonoesioides jacobyi* Freund & Wagner, 2003 (**9**) ♂ HT: Habitus in dorsal view.

COL 2006/187 **1 ♀ AT**
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)
COL 2006/186 **1 ♂ PT**
October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)

muehlei Frieser, 1997: 15 *(Uncifer)*
COL 2006/175 **1 ♂ PT**
Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`W 11.-20.VII.95 - Th. Wagner leg. / T.n.15 1 / Paratype / Uncifer muehlei sp. n. - Paratypus ♂ - det. R. Frieser 1996
11.-20. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (exact gathering site information; error on original label!)

nubilus Frieser, 1997: 15-16 *(Uncifer)*
COL 2006/176 **♂ HT** **(Fig. 2)**
Uganda, District Masindi - Budongo Forest n: Sonso - 1°45`N, 31°35`W 1.-10.VII.95 - Th. Wagner leg. / Holotype / Uncifer nubilus sp. n. - Holotypus ♂ - det. R. Frieser 1996
01.-10. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (exact gathering site information; error on original label!)
COL 2006/177 **1 ♀ AT**
21.-30. July 1995
COL 2006/178 **1 ♂ PT**
11.-20. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (exact gathering site information; error on original label!)

proprius Frieser, 1997: 16 *(Uncifer)*
COL 2006/179 **♂ HT** **(Fig. 3)**
Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`W 21.-30.VII.95 - Th. Wagner leg. / T.n.11/2 / Holotype / Uncifer proprius sp. n. - Holotypus ♂ - det. R. Frieser 1996
21.-30. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (exact gathering site information; error on original label!)
COL 2006/180 **1 ♀ AT**
COL 2006/181, 184 **2 ♂ PT**
11.-20. July 1995
COL 2006/183 **1 ♂ PT**
COL 2006/182 **1 ♀ PT**
21.-30. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (exact gathering site information; error on original label!)

CERAMBYCIDAE

wagneri Adlbauer, 2006: 20-21 *(Stathmodera)*
Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi
COL 2006/688 **1 PT**
Kenya, Kakamega F., - 0°22`N/34°50`E, 1800 m, - 7-11.II.99 Th. Wagner leg. / T.n.33 1 / PARATYPUS STATHMODERA - wagneri - ADLBAUER, 2006
7.-11. Februay 1999
Kakamega Forest, Western, Kenya, Africa
0°17`N, 34°53`E (exact gathering site information; imprecise data on original label!)
COL 2006/689 **1 PT**
January 2002
COL 2006/696 **1 PT**
October 2002
Isiukhu River, Kakamega Forest, Western, Kenya, Africa
0°20`N, 34°53`E (exact gathering site information; imprecise data on original label!)
COL 2006/690-691 **2 PT**
January-Februay 2002
COL 2006/692 - 695 **4 PT**
October 2002
COL 2006/701 **1 PT**
January 2003
Busumbuli River, Kakamega Forest, Western, Kenya, Africa
0°19`N, 34°52`E (exact gathering site information; imprecise data on original label!)
COL 2006/697 - 698 **2 PT**
October 2002
COL 2006/702 **1 PT**
January 2003
Colobus Trail, Kakamega Forest, Western, Kenya, Africa
0°21`N, 34°51`E (exact gathering site information; imprecise data on original label!)
COL 2006/699 **1 PT**
October 2002
Kisere Forest, Kakamega Forest, Western, Kenya, Africa
0°24`N, 34°54`E (site information)
COL 2006/700 **1 PT**
October 2002
Yala River, Kakamega Forest, Western, Kenya, Africa
0°12`N, 34°53`E (exact gathering site information; imprecise data on original label!)

CHRYSOMELIDAE

alwineae Wagner, 2002: 35 *(Monolepta)*
COL 2007/156 **♂ HT** **(Fig. 4)**
Ivory Coast, Comoe - NP, 8,75N / 3,80W - VI.-VII.1997, C. Mody leg. / KC 35 .1C III.15 / Holotypus / Monolepta - alwineae sp. nov. - Th. Wagner det. 02 / AfriGa - specimen ID - 1270 - specimen data - documented - 23.III.2006
June-July 1997
Komoe, Parc National de la, Zanzan, Cote d'Ivoire, Africa
8°45`N, 3°48`W (site information)

budongoensis Wagner, 2002: 29 *(Monolepta)*

COL 2007/157 ♂ HT (Fig. 5)

Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`E; - 21.-30.VII.95 - Th. Wagner leg. / R.a.22 1 / Holotypus / Monolepta - budongoensis - Wag-ner / AfriGa - specimen ID - 1266 - specimen data - documented - 23.III.2006
21.-30. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (site information)

COL 2006/158-159 2 PT

5.-12. Februay 1997
Semliki Forest, Bundibugyo, Western, Uganda, Africa
0°48`N, 30°08`E (site information)

clarae Wagner, 2000a: 36 *(Monolepta)*

COL 2007/160 1 ♂ PT

Congo Belge, P.N.G. - Miss. H. De Saeger - Ndelele/2, 6-VI-1952 - H. De Saeger. 3589 / Paratypus / Monolepta clarae - Wagner, 1999 - Th. Wagner det.
6. June 1952
Ndelele (mts.), Garamba, Parc National de la, Haut-Congo, Democratic Republic of the Congo, Africa
4°22`N, 29°47`E (gathering site: estimated value)

COL 2006/161 1 ♂ PT

20. June 1952
PFSK.5, Garamba, Parc National de la, Haut-Congo, Democratic Republic of the Congo, Africa
4°10`N, 29°30`E (gathering site: estimated value)

COL 2006/162 1 ♂ PT

22. June 1952
Utukuru (river), Garamba, Parc National de la, Haut-Congo, Democratic Republic of the Congo, Africa
4°19`N, 29°52`E (gathering site: estimated value)

clasnaumanni Wagner, 2001b: 62 *(Monolepta)*

COL 2007/163 1 PT

I.R.S.A.C.-Mus.Congo - Kivu : Terr. Masisi, Lacs - Mokoto, 1800 m. - B. 82 N. Leleup VI-1959 / Bior. N° 81 - Humus - en foret / Paratype - Monolepta - clausnaumanni
June 1959
Lacs Mokoto (lake), Masisi, Nord-Kivu, Democratic Republic of the Congo, Africa
1°16`S, 29°00`E (gathering site: estimated value)

comoeensis Wagner, 2000b: 235 *(Monolepta)*

COL 2007/164 ♂ HT (Fig. 6)

Ivory Coast, Comoe - NP, 8,75N / 3,80W - IX.1999, C. Mody leg. / Holotypus / Monolepta - comoeensis - Wagner / AfriGa - specimen ID - 1296 - specimen data - documented - 23.III.2006
September 1999
Komoe, Parc National de la, Zanzan, Cote d'Ivoire, Africa
8°45`N, 3°48`W (site information)

COL 2006/165-190 26 PT

September 1999
Komoe, Parc National de la, Zanzan, Cote d'Ivoire, Africa
8°45`N, 3°48`W (site information)

congoensis Wagner, 2002: 33 *(Monolepta)*

COL 2007/192 ♂ HT (Fig. 7)

Uganda, Semliki Forest - 0°48`N, 30°8`E; 5.-12.II.97 - Th. Wagner leg. / C.a. S4 1 / Holotypus / Monolepta - congoensis - Wagner / AfriGa - specimen ID - 1267 - specimen data - documented - 23.III.2006
5.-12. Februay 1997
Semliki Forest, Bundibugyo, Western, Uganda, Africa
0°48`N, 30°08`E (site information)

constantini Wagner, 2000a: 34 *(Monolepta)*

COL 2007/193 ♂ HT (Fig. 8)

Uganda, Dtr. Mbale - Budadiri, 1240 m, 1°10`N, 34°20`E - Th. Wagner leg. 21.IX.1997 / Holotypus / Monolepta - constantini - Wagner, 2000 - Holotypus / AfriGa - specimen ID - 1289 - specimen data - documented - 23.III.2006
21. September 1997
Budadiri, Sironko, Northern, Uganda, Africa
1°10`N, 34°20`E (site information)

COL 2006/194 1 ♂ PT

18. June 1952
Iso, Garamba, Parc National de la, Haut-Congo, Democratic Republic of the Congo, Africa
4°10`N, 29°30`E (gathering site: estimated value)

COL 2006/195 1 ♂ PT

20. April 1952
Embe (mts.), Garamba, Parc National de la, Haut-Congo, Democratic Republic of the Congo, Africa
4°40`N, 29°31`E (gathering site: estimated value)

decellei Wagner, 2002: 34 *(Monolepta)*

COL 2007/225 1 PT

Coll. Mus. Tervuren - Cote d'Ivoire: Mouyassue, - 30 km, E.d'Aboisso - J. Decelle VI.1961 / Récolté sur - cacaoyer / Paratypus / Monolepta - decellei Wagner
June 1961
Mouyassue, Aboisso, Sud-Comoé, Cote d'Ivoire, Africa

COL 2006/226 1 PT

20. April 1952
Embe (mts.), Garamba, Parc National de la, Haut-Congo, Democratic Republic of the Congo, Africa
4°40`N, 29°31`E (gathering site: estimated value)

ephippiatoides Wagner, 2001a: 206 *(Monolepta)*

COL 2007/227-229 3 PT

SÜDAFRIKA, NE-Prov. - Tshipise, Honet Nature - Reserve Berg b. Camp - 22°37`S, 30°10`E, 320 m - NN, 23.-25.XI.1996 - leg. M. Hartmann / Paratypus / Monolepta - ephippiatoides - Wagner
23.-25. November 1996

Tshipise, Transvaal, Northern Province, South Africa, Africa
22°37`S, 30°10`E (site information)

gerstaeckeri Wagner, 2001a: 200 *(Monolepta)*

COL 2007/196-197 **2 ♂ PT**

Musee du Congo - Kapiri - IX-1912 - Miss. Agric. / Paratypus / Monolepta - gerstaeckeri - Wagner
September 1912
Kapiri, Katanga, Democratic Republic of the Congo, Africa
10°18`S, 26°10`E (gathering site: estimated value)

COL 2006/198 **1 PT**

Kundelungus, Katanga, Democratic Republic of the Congo, Africa
10°00`S, 28°00`E (gathering site: estimated value)

hartmanni Wagner, 2000b: 233 *(Monolepta)*

COL 2007/199 **1 PT**

Shilouvane - "C ?" habina - Zoutpansberg - H. Junod / unlesbare Etikett / Musee du Congo - Transvall: - Zoutpansberg - Coll. Clavareau / R. Det. - L - 3678 / Paratypus / Monolepta - hartmanni Wagner / coll. - Th. Wagner
Zoutpansberg(= Soutpansberg), Transvaal, 'Northern Province, South Africa, Africa
22°58`S, 29°45`E (gathering site: estimated value)

COL 2006/200 **1 ♂ PT**

19. December 1972
Macheke, Mashonaland East, Zimbabwe, Africa
18°09`S, 31°51`E (gathering site: estimated value)

ivorensis Wagner, 2001b: 55 *(Monolepta)*

COL 2007/201 **1 ♂ PT**

Coll. Mus. Tervuren - Cote d'Ivoire: Heremankono, - au sud de Divo - J. Decelle VIII.1961 / Paratypus / Monolepta - ivorensis - Th. Wagner
August 1961
Heremankono, Forest, Divo, Sud-Bandama, Cote d'Ivoire, Africa
5°49`S, 5°00`W (gathering site: estimated value)

COL 2006/202-204 **3 PT**

June 1961
Mouyassue, Aboisso, Sud-Comoé, Cote d'Ivoire, Africa

jacobyi Freund & Wagner, 2003: 1953 *(Bonesioides)*

COL 2007/191 **♂ HT** **(Fig. 9)**

Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`E; - 19.-30.VI.95 - Th. Wagner leg. / Holotypus - Bonesioides - jacobyi / Bonesioides - jacobyi - Freund & Wagner 2000 / AfriGa - specimen ID - 1642 - specimen data - documented - 23.III.2006
19.-30. June 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (site information)

kakamegaensis Middelhauve & Wagner, 2001: 526 *(Afrocrania)*

Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi

COL 2007/231 -234 **5 PT**

Kenya, Kakamega F., - 0°22`N/34°50`E, 1600m, - 7-11.II.99, Th. Wagner leg. / Paratypus - Afrocrania - kakamegaensis - Middelhauve & Wagner
7.-11. Februay 1999
Kakamega Forest, Western, Kenya, Africa
0°17`N, 34°53`E (exact gathering site information; imprecise data on original label!)

laboissierei Wagner, 2001a: 201 *(Monolepta)*

COL 2007/205-207 **3 PT**

Coll. Mus. Congo - Lulua: Kapanga - X.1933 - G.F. Overlaet / Paratypus / Monolepta - laboissierei Wagner / coll. – Th. Wagner
October 1933
Kapanga, Lulua, Kasai Occidental, Democratic Republic of the Congo, Africa
8°13`S, 22°22`E (gathering site: estimated value)

COL 2006/208-209 **2 PT**

20. October 1951

COL 2006/210 **1 PT**

12. April 1952

COL 2006/211 **1 PT**

18. July 1952
Garamba, Parc National de la, Haut-Congo, Democratic Republic of the Congo, Africa
4°10`N, 29°30`E (gathering site: estimated value)

marcoi Freund & Wagner, 2003: 1957 *(Bonesioides)*

COL 2007/230 **1 PT**

Uganda, Semliki Forest - 0°48`N, 30°8`E; 5.-12.II.97 - Th. Wagner leg. / C.a. S7 1 / Paratypus / Bonesioides - marcoi - Freund & Wagner
5.-12. Februay 1997
Semliki Forest, Bundibugyo, Western, Uganda, Africa
0°48`N, 30°08`E (site information)

mpangae Wagner, 2000a: 38 *(Monolepta)*

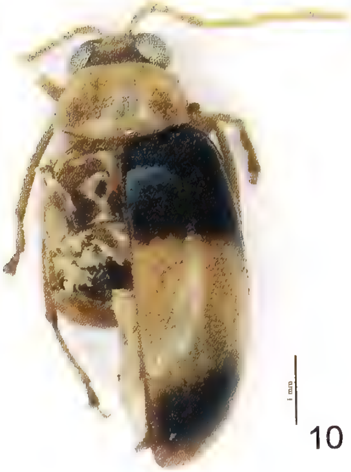
COL 2007/212-213 **2 ♂ PT**

Uganda Prot. - Mpanga Forest, - Toro. 4,800 ft. - 13-23 Nov. 1911. - S. A. Neave. / 1912-193 / Paratypus / Monolepta mpangae - Wagner - Th. Wagner det. 1999
13.-23. November 1911
Mpanga Forest (forest), Central, Uganda, Africa
0°12`N, 32°18`E (gathering site: estimated value)

naumanni Wagner, 2005: 279 *(Monolepta)*

COL 2007/214 **♂ HT** **(Fig. 10)**

Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`E; 1.-10.VII.95 - Th. Wagner leg. / T.r.15 2 / Holotypus / Monolepta - naumanni sp. nov. - Th. Wagner / AfriGa - specimen ID - 1835 - specimen data - documented - 23.III.2006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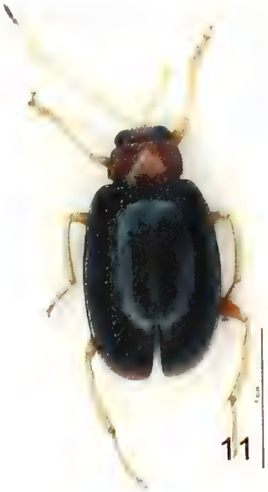
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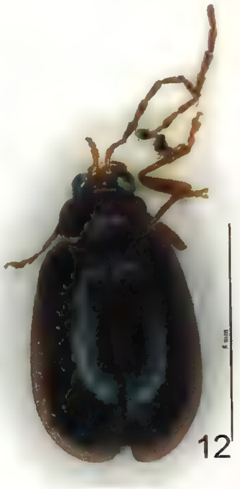
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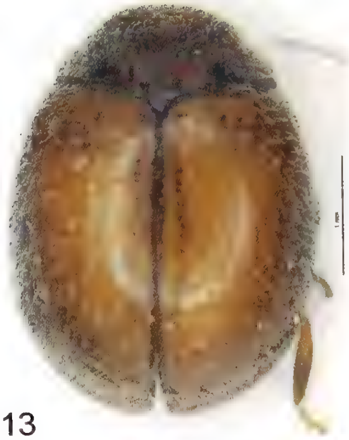
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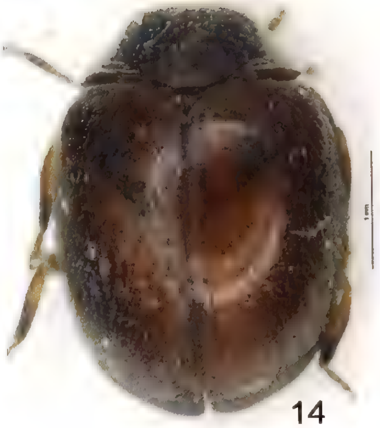
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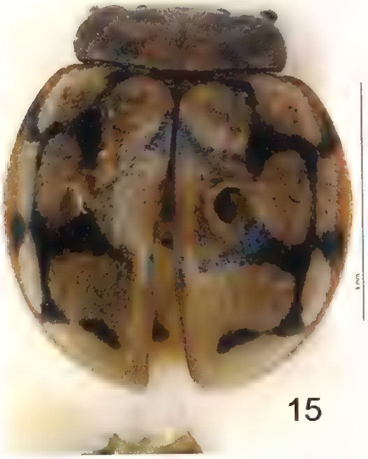
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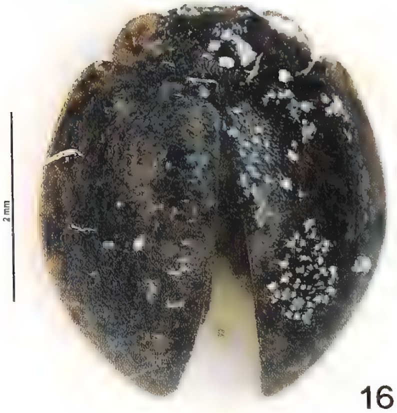
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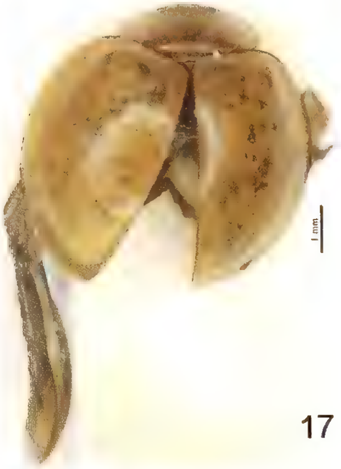
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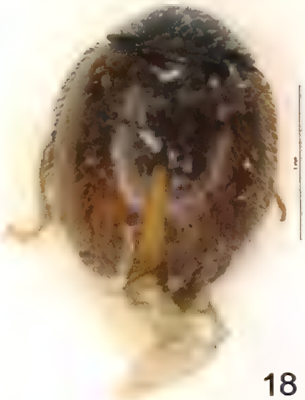

18

Figs 10–18. *Monolepta naumanni* Wagner, 2005 **(10)** ♂ HT, *Monolepta peleae* Wagner, 2003 **(11)** ♂ HT, *Monolepta sonsoensis* Wagner, 2001 **(12)** ♂ HT, *Nephus brevipilosus* Fürsch, 1997 **(13)** ♂ HT, *Pseudoscymnus brunneus* Fürsch, 1997 **(14)** ♂ HT, *Epilachna carapacola* Fürsch, 1997 **(15)** ♂ HT, *Epilachna conspergata* Fürsch, 1997 **(16)** ♂ HT, *Harmonia gilvella* Fürsch, 2001 **(17)** ♂ HT, *Scotoscymnus glabripilosus* Fürsch, 1997 **(18)** ♂ HT: Habitus in dorsal view.

1.-10. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (site information)

COL 2007/244-245 2 PT
1.-10. July 1995

COL 2007/246-247 2 PT
11.-20. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (site information)

COL 2007/248 1 PT
5.-12. Februay 1997
Semliki Forest, Bundibugyo, Western, Uganda, Africa
0°48`N, 30°08`E (site information)

COL 2006/251 1 PT
January 2003
Busumbuli River, Kakamega Forest, Western, Kenya, Africa
0°19`N, 34°52`E (exact gathering site information; imprecise data on original label!)

COL 2006/253 1 PT
October 2002
Colobus Trail, Kakamega Forest, Western, Kenya, Africa
0°21`N, 34°51`E (exact gathering site information; imprecise data on original label!)

COL 2006/252 1 PT
January 2003
Kisere Forest, Kakamega Forest, Western, Kenya, Africa
0°24`N, 34°54`E (site information

COL 2007/249 1 PT
November 2001

COL 2007/250 1 PT
January 2003
Yala River, Kakamega Forest, Western, Kenya, Africa
0°12`N, 34°53`E (exact gathering site information; imprecise data on original label!)

peleae Wagner, 2003: 80 *(Monolepta)*

COL 2007/215 ♂ HT (Fig. 11)
Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / T.n.1 1 / Holotypus / Monolepta - peleae - sp. nov. Th. Wagner / AfriGa - specimen ID - 1708 - specimen data - documented - 23.III.2006
October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa
2°15` S, 30°50`E (gathering site: estimated value)

COL 2006/216 1 PT
1893
Pretoria, Transvaal, Northern Province, South Africa, Africa
25°45`S, 28°10`E (gathering site: estimated value)

COL 2006/217 1 PT
30. July – 2. August 2000
Peramiho, Ruvuma, Tanzania, Africa
10°39`S, 35°27`E (gathering site: estimated value)

sonsoensis Wagner, 2001b: 54 *(Monolepta)*

COL 2007/218 ♂ HT (Fig. 12)
Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`E; 1.-10.VII.95 - Th. Wagner leg. / Holotypus / Monolepta - sonsoensis Wagner / AfriGa - specimen ID – 1276 - specimen data - documented - 23.III.2006
1.-10. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (site information)

COL 2006/219 1 PT
1.-10. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (site information)

tutseki Wagner & Scherz, 2002: 359 *(Afrocandezea)*

Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi

COL 2007/235 1 PT
Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`W; - 19.-30.VI.95 - Th. Wagner leg. / Paratypus / Afrocandezea tutseki - sp. nov. - Scherz & Wagner 2002
19.-30. June 1995

COL 2007/236 1 PT
11.-20. July 1995

COL 2007/237 1 PT
5.-15. January 1997

COL 2007/238-239 2 PT
September 1997
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (exact gathering site information; error on original label!)

COL 2007/240-243 4 PT
26. July – 22. August 1998
Kanyawara (Kibale National Park), Kabarole, Western, Uganda, Africa
0°34`N, 30°20`E (gathering site: estimated value)

upembaensis Wagner, 2000b: 234 *(Monolepta)*

COL 2007/220 1 PT
Congo belge: P.N.U. - Mbuye-Bala (1750 m.) - 1-7-IV-1948 - Mis. G.F. de Witte. 1500a / Paratypus / Monolepta - upembaensis - Wagner / coll. - Th. Wagner
1.-7. April 1948
Mbuye-Bala (stream)(= Buye-Bala (stream)), Upemba, Parc National de la, Katanga, Democratic Republic of the Congo, Africa
8°54`S, 26°59`E (gathering site: estimated value)

ursulae Wagner, 2003: 67 *(Monolepta)*

COL 2007/221, 257-258 3 PT
S.W. - AFRIKA - Okahandja I.1956. - W. Hoesch leg., ded. - Eing.Nr.6, 1956. / Paratypus / Monolepta - ursulae - Th. Wagner
January 1956

Okahandja, Okahandja, Otjozondjupa, Namibia, Africa
21°59`S, 16°5`E (gathering site: estimated value)
COL 2006/224, 265-267 **3 PT**
12. January 1985
COL 2006/268-270 **3 PT**
27. March 1988
Döbra, Windhoek, Khomas, Namibia, Africa
22°20`S, 17°06`E (gathering site: estimated value)
COL 2006/271 **1 PT**
14.-22. January 1982
Kombat, Grootfontein, Otjozondjupa, Namibia, África
19°43`S, 17°43`E (gathering site: estimated value)
COL 2006/272 **1 PT**
20. February - 6. March 1979
Gobabeb, Swakopmund, Erongo, Namibia, Africa
23°33`S, 15°02`E (gathering site: estimated value)
COL 2006/223 , 264 **2 PT**
9.-15. March 1985
Naos, Rehoboth, Hardap, Namibia, Africa
23°12`S, 16°46`E (gathering site: estimated value)
COL 2006/261 **1 PT**
15. December 1974
COL 2006/262 **1 PT**
8.-12. March 1979
COL 2006/222, 259-260 **3 PT**
8.-13. January 1982
COL 2006/263 **1 PT**
17.-20. March 1982
Okahandja, Okahandja, Otjozondjupa, Namibia, Africa
21°59`S, 16°5`E (gathering site: estimated value)
COL 2006/273 **1 PT**
18.-20. March 1991
Osona, Okahandja, Otjozondjupa, Namibia, Africa
22°04`S, 16°53`E (gathering site: estimated value)
COL 2006/274 **1 PT**
7. February 1975
COL 2006/275-276 **2 PT**
8. February 1975
COL 2006/273 **1 PT**
2. March 1975
Windhoek, Windhoek, Khomas, Namibia, Africa
22°35`S, 17°05`E (gathering site: estimated value)

COCCINELLIDAE

brevipilosus Fürsch, 1997: 18 *(Nephus)*
COL 2006/13 **♂ HT** **(Fig. 13)**
Rwanda, Nyakabuye - Cyamudongo X.93 - Th. Wagner leg. / C.g. 12 / Holotypus - Nephus ♂ - brevipilosus - Fürsch, 1995
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)
COL 2006/14 **1 ♂ PT**
October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)
COL 2006/15-16 **2 ♀ PT**
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

brunneus Fürsch, 1997: 20 *(Pseudoscymnus)*
COL 2006/53 **♂ HT** **(Fig. 14)**
Rwanda, Nyakabuye - Cyamudongo X.93 - Th. Wagner leg. / Cg II / Holotypus - Pseudoscymnus - brunneus ♂ - Fürsch, 1995
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)
COL 2006/54-55, 57-60 **6 ♀ PT**
COL 2006/56, 61 **2 ♂ PT**
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

carapacola Fürsch, 1997: 26 *(Epilachna)*
COL 2006/41 **♂ HT** **(Fig. 15)**
Rwanda, 1700 m - Cyamudongo, X.93 - Th. Wagner leg. / C.g. 17 1 / Holotypus - Epilachna ♂ - carapacola - Fürsch, 95
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)
COL 2006/42 **1 ♀ PT**
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

conspergata Fürsch, 1997: 24 *(Epilachna)*
COL 2006/43 **♂ HT** **(Fig. 16)**
Rwanda, Nyungwe - Kamiranzovu, 2000 m - Th. Wagner leg. X.93 / C.g. 2 4 / Holotypus - Epilachna ♂ - conspergata - Fürsch, 95
October 1993
Kamiranzovu, Nyungwe Forest, Cyangugu, Rwanda, Africa
2°29`S, 29°09`E (gathering site: estimated value)
COL 2006/44 **1 ? PT**
COL 2006/45 **1 PT**
October 1993
Kamiranzovu, Nyungwe Forest, Cyangugu, Rwanda, Africa
2°29`S, 29°09`E (gathering site: estimated value)
COL 2006/46 **1 ♀ PT**
October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)

fissilobis Fürsch, 2001b: 103-104 *(Pharoscymnus)*

Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi

COL 2006/107-115 9 PT

Kenya, Nairobi, Langata, - 1°20`S/36°46`E, 1650 m, 12.-14.I.1999, - Th. Wagner leg. / T.s.4 4 / Paratypus - Pharoscymnus - fissilobis - Fürsch, 1999
12.-14. January 1999
Langata (Nairobi), Nairobi, Kenya, Africa
1°20`S, 36°46`E (site information)

gilvella Fürsch, 2001b: 98-99 *(Harmonia)*

COL 2006/1185 ♂ HT (Fig. 17)

Uganda, Semliki Forest - 0°48' N, 30°8' E; 5.-12.II.97 - Th. Wagner leg. / C.a. S3 7 / Holotypus - Micraspis ♂ - gilvella - Fürsch, 1999
5.-12. Februay 1997
Semliki Forest, Bundibugyo, Western, Uganda, Africa
0°48`N, 30°08`E (site information)

COL 2006/6-8, 1186-1190 8 PT

5.-12. Februay 1997
Semliki Forest, Bundibugyo, Western, Uganda, Africa
0°48`N, 30°08`E (site information)

glabripilosus Fürsch, 1997: 22 *(Scotoscymnus)*

COL 2006/62 ♂ HT (Fig. 18)

Rwanda, 1700 m - Karengera, X.93 - Th. Wagner leg. / C.g.1 14 / Holotypus - Scotoscymnus - glabripilosus ♂ - Fürsch, 1995
October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)

COL 2006/63-64, 70, 73, 75-80 10 PT

October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

COL 2006/65, 67-69, 81 5 PT

October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)

COL 2006/66, 72, 74 3 PT

October 1993
Kamiranzovu, Nyungwe Forest, Cyangugu, Rwanda, Africa
2°29`S, 29°09`E (gathering site: estimated value)

COL 2006/71 1 PT

October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa
2°15`S, 30°50`E (gathering site: estimated value)

gracilis Fürsch, 1997: 20 *(Ortalia)*

COL 2006/5 ♂ HT (Fig. 19)

Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / Holotypus - Ortalia - gracilis ♂ - Fürsch, 95 / Ortalia basinigra Ma. - det. H. Fürsch 03
October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa
2°15`S, 30°50`E (gathering site: estimated value)

goellnerae Fürsch, 2001b: 100 *(Platynaspis)*

COL 2007/58-59 2 ♀ PT

Uganda, Semliki Forest - 0°48`N, 30°8`E; 5.-12.II.97 - Th. Wagner leg. / Paratype - Platynaspis - goellnerae ♀ - Fürsch, 1999
5.-12. Februay 1997
Semliki Forest, Bundibugyo, Western, Uganda, Africa
0°48`N, 30°08`E (site information)

kenyensis Fürsch, 2001b: 101-102 *(Boschalis)*

Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi

COL 2006/116 1 PT

Mt. Kenya, NP-HQ, - 2550 m, 0°10.5`S/37°8.8`E; - II.99 Th. Wagner leg. / P.l.17 2 / Paratypus - Boschalis kenyensis - Fürsch, 99
Februay 1999
Mount Kenya (mts.), Central, Kenya, Africa
0°10`S, 37°11`E (exact gathering site information; imprecise data on original label!)

COL 2006/117 1 PT

January 1999
Gatamayu, Kikuyu, Central, Kenya, Africa
0°58`S, 36°42`E (site information)

COL 2006/118 1 PT

18. Februay 1999
SE-Aberdare, Central, Kenya, Africa
0°23`S, 36°46`E (site information)

magnifica Fürsch, 2006: 114-115 *(Cheilomenes)*

COL 2007/56 ♂ HT (Fig. 20)

Kenya, Busumbuli, 1600 m - Kakamega Forest - 0,27°N / 34,88°E - W. Freund leg. X.01 / T.n.138 1 - IX.-X.2001 / Holotypus - Cheilomenes - magnifica ♂ - Fürsch, 2005
October 2001
Busumbuli River, Kakamega Forest, Western, Kenya, Africa
0°19`N, 34°52`E (exact gathering site information; imprecise data on original label!)

COL 2007/57 1 ♀ PT

January 2003
Kisere Forest, Kakamega Forest, Western, Kenya, Africa
0°24`N, 34°54`E (site information)

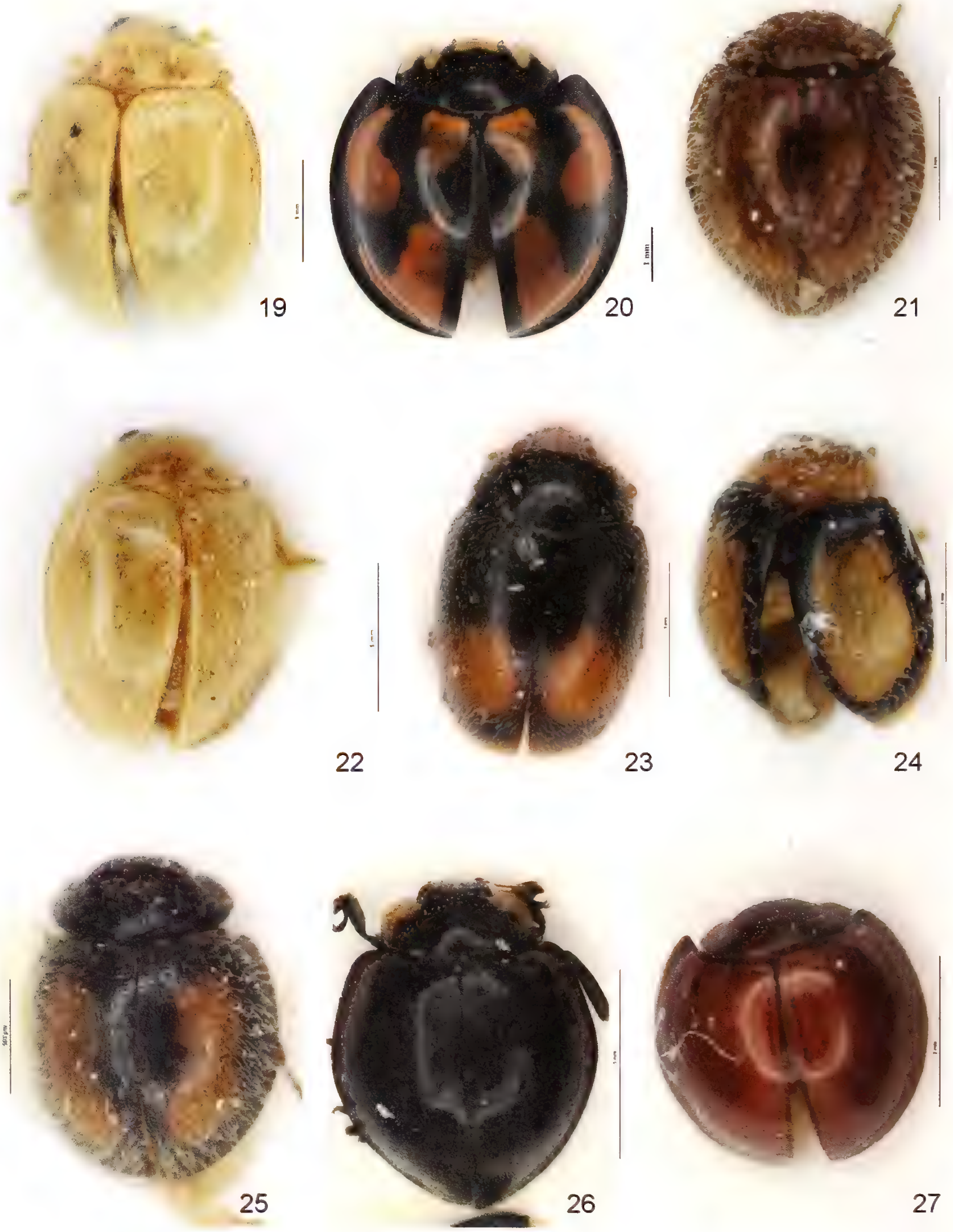
maximus Fürsch, 1997: 22-24 *(Scotoscymnus)*

COL 2006/87 ♂ HT (Fig. 21)

Rwanda, Nyakabuye - Cyamudongo X.93 - Th. Wagner leg. / Cg 9 / Holotypus ♂ - Scotoscymnus - maximus - Fürsch, 95
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

COL 2006/88, 90-106 18 PT

October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)



Figs 19–27. *Ortalia gracilis* Fürsch, 1997 (**19**) ♂ HT, *Cheilomenes magnifica* Fürsch, 2006 (**20**) ♂ HT, *Scotoscymnus maximus* Fürsch, 1997 (**21**) ♂ HT, *Ortalia minima* Fürsch, 2001 (**22**) ♂ HT, *Nephus rugulipennis* Fürsch, 1997 (**23**) ♂ HT, *Scymnus rwandensis* Fürsch, 1997 (**24**) ♂ HT, *Telsimia striata* Fürsch, 1997 (**25**) ♂ HT, *Epilachna struwei* Fürsch, 2001 (**26**) ♂ HT, *Boschalis wagneri* Fürsch, 1997 (**27**) ♂ HT: Habitus in dorsal view.

COL 2006/89 **1 PT**
October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)

minima Fürsch, 2001b: 99 *(Ortalia)*
COL 2006/4 **♂ HT** **(Fig. 22)**
Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`E; 15.-25.I.97 - Th. Wagner leg. / C.a.35 1 / Holotypus - Ortalia ♂ - minima - Fürsch, 1999
15.-25. January 1997
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (site information)

montivagans Fürsch, 2001a: 91-92 *(Nephus)*
Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi
COL 2006/9,11 **2 PT**
Mt. Kenya, NP-HQ, - 2550 m, 0°10.5`S, 37°8.8`E; - II.99 Th. Wagner leg. / Av 16 2 / Paratypus - Nephus - montivagans - Fürsch, 1999
Februay 1999
Mount Kenya (mts.), Central, Kenya, Africa
0°10`S, 37°11`E (exact gathering site information; imprecise data on original label!)
COL 2006/10 **1 PT**
18. Februay 1999
SE-Aberdare, Central, Kenya, Africa
0°23`S, 36°46`E (site information)

rubida Fürsch, 2001b: 104 *(Epilachna)*
Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi
COL 2006/31-40 **10 PT**
Mt. Kenya, Chogoria Rte., - 0°09`S/37°26`E, 2800 m, - 25.II.1999, Th. Wagner leg. / Paratype - Epilachna - rubida - Fürsch, 2000
25. Februay 1999
Chogoria Rte., Mount Kenya (mts.), Eastern, Kenya, Africa
0°09`S, 37°26`E (site information)

rubridorsis Fürsch, 2001a: 92-93 *(Nephus)*
Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi
COL 2006/17 **1 ♀ PT**
Kenya Kikuyu, Gatamayu - 2330 m 0°58`S/36°42`E, - 2.99 leg. Th. Wagner / Paratypus - Nephus (Sidis) - rubridorsis ♀ - Fürsch 2000
Februay 1999
Gatamayu, Kikuyu, Central, Kenya, Africa
0°58`S, 36°42`E (site information)

rugulipennis Fürsch, 1997: 18 *(Nephus)*
COL 2006/12 **♂ HT** **(Fig. 23)**
Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / Holotypus - Nephus ♂ - rugulipennis - Fürsch, 1995
October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Ăfrica
2°15`S, 30°50`E (gathering site: estimated value)

rwandensis Fürsch, 1997: 16 *(Scymnus)*
COL 2006/47 **♂ HT** **(Fig. 24)**
Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / T.n.5 3 / Holotypus - Scymnus (Pullus) - rwandensis ♂ - Fürsch, 1995
October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa
2°15`S, 30°50`E (gathering site: estimated value)
COL 2006/48 - 52 **5 PT**
October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa
2°15`S, 30°50`E (gathering site: estimated value)

striata Fürsch, 1997: 20-22 *(Telsimia)*
COL 2006/131 **♂ HT** **(Fig. 25)**
Rwanda, 1700 m - Cyamudongo, X.93 - Th. Wagner leg. / C.g.4 2 / Holotypus - Telsimia - striata ♂ - Fürsch, 1995
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)
COL 2006/132 **1 ♀ PT**
COL 2006/133-134 **2 PT**
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

struwei Fürsch, 2001b: 105-106 *(Epilachna)*
COL 2006/125 **♂ HT** **(Fig. 26)**
Rwanda, Mont - Bisoke, X.92 / Holotypus - Epilachna - struwei ♂ - Fürsch, 1999
October 1992
Volcano Visoke (Bisoko), Volcano National Park, Ruhengeri, Rwanda, Africa
1°28`S, 29°29`E (gathering site: estimated value)
COL 2006/126-130 **5 PT**
October 1992
Volcano Visoke (Bisoko), Volcano National Park, Ruhengeri, Rwanda, Africa
1°28`S, 29°29`E (gathering site: estimated value)

vulpecula Fürsch, 2001a: 93 *(Nephus)*
Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi
COL 2006/18, 29 **2 PT**
Kenya, Kikuyu, Gatamayu, - 2330 m 0°58`S/36°42`E - II.99 Th. Wagner leg. / P.l.4 2 / Paratypus - Nephus - vulpecula - Fürsch, 1999
Februay 1999
Gatamayu, Kikuyu, Central, Kenya, Africa
0°58`S, 36°42`E (site information)
COL 2006/19-28, 30 **11 PT**
18. Februay 1999
SE-Aberdare, Central, Kenya, Africa
0°23`S, 36°46`E (site information)

wagneri Fürsch, 1995: 30 *(Boschalis)*

COL 2006/119 **♂ HT** **(Fig. 27)**
Rwanda, Nyakabuye - Cyamudongo X.93 - Th. Wagner leg. / C.g.9 3 / Holotype - Boschalis - wagneri ♂ - Fürsch, 1995
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

COL 2006/120-124 **5 PT**
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

wagneri Fürsch, 2001b: 103 *(Scotoscymnus)*
Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi, 3 paratypes dto.

COL 2006/82-86 **5 PT**
Kenya, SE-Aberdare, - 0°23`S/36°46`E, 2750 m, - 18.II.99 Th. Wagner leg. / P.I. 263 / Paratypus – Scotoscymnus - wagneri - Fürsch, 1999
18. Februay 1999
SE-Aberdare, Central, Kenya, Africa
0°23`S, 36°46`E (site information)

wagneri Fürsch, 2006a: 116; 2006b: 266 *(Stethorus)*
Holotype ♂ - in: National Museums of Kenya (NMK), Nairobi, 32 paratypes dto.

COL 2007/60-65 **6 PT**
Kenya, Kakamega F., - 0°22`N/34°50`E, 1600 m, - 7-11.II.99, Th. Wagner leg. / Paratypus - Stethorus - wagneri - Fürsch, 2005
7.-11. Februay 1999
Kakamega Forest, Western, Kenya, Africa
0°17`N, 34°53`E (exact gathering site information; imprecise data on original label!)

COL 2007/66 **1 PT**
October 2002
Busumbuli River, Kakamega Forest, Western, Kenya, Africa
0°19`N, 34°52`E (exact gathering site information; imprecise data on original label!)

COL 2007/67-68 **2 PT**
October 2001

COL 2007/69-74 **6 PT**
January 2002

COL 2007/75 **1 PT**
October 2002

COL 2007/76-78 **3 PT**
January 2003
Colobus Trail, Kakamega Forest, Western, Kenya, Africa
0°21`N, 34°51`E (exact gathering site information; imprecise data on original label!)

COL 2007/79 **1 PT**
January 2002

COL 2007/80-81 **2 PT**
January 2003
Isiukhu River, Kakamega Forest, Western, Kenya, Africa
0°20`N, 34°53`E (exact gathering site information; imprecise data on original label!)

COL 2007/82-84 **3 PT**
January 2002

COL 2007/85-86 **2 PT**
October 2002

COL 2007/87-88 **2 PT**
January 2003
Kisere Forest, Kakamega Forest, Western, Kenya, Africa
0°24`N, 34°54`E (site information)

COL 2007/89-94 **6 PT**
January 2002

COL 2007/95-97 **3 PT**
January 2003
Yala River, Kakamega Forest, Western, Kenya, Africa
0°12`N, 34°53`E (exact gathering site information; imprecise data on original label!)

DERMESTIDAE

rusumoensis Háva & Herrmann, 2002: 254 *(Orphinus)*

COL 2007/254 **♂ HT** **(Fig. 28)**
Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / Holotypus - Orphinus (Orphinus) - rusumoensis n. sp. ♂ - det. J. Háva & A. Herrmann 2002
October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa
2°15`S, 30°50`E (gathering site: estimated value)

wagneri Háva & Herrmann, 2002: 253 *(Orphinus)*

COL 2007/255 **♂ HT** **(Fig. 29)**
Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / Holotypus - Orphinus (Orphinus) - wagneri n. sp. ♂ - det. J. Háva & A. Herrmann 2002
October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa
2°15`S, 30°50`E (gathering site: estimated value)

HYDROPHILIDAE

magnus Hebauer, 2002b: 6 *(Allocotocerus)*

COL 2006/135-136 **2 PT**
Kenya, Kakamega F., - 0°22`N/34°50`E, 1600 m, - 7-11.II.99, Th. Wagner leg. / Paratypus - Allocotocerus - magnus sp. n. - des. F. Hebauer
7.-11. Februay 1999
Kakamega Forest, Western, Kenya, Africa
0°17`N, 34°53`E (exact gathering site information; imprecise data on original label!)

COL 2006/137-138 **2 PT**
05.-15. Jan. 1997
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (site information)

melinus Hebauer, 2001: 384 *(Enochrus)*

COL 2006/141 **1 PT**

Uganda District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`W 19.-30.VI.95 - Th. Wagner leg. / Paratypus / Enochrus (Meth.) - melinus sp. n. - det. F. HEBAUER

19.-30. June 1995

Sonso River (Budongo Forest), Masindi, Uganda, Africa

1°45`N, 31°35`E (exact gathering site information; error on original label!)

perssoni Hebauer, 2002a: 267 *(Enochrus)*

COL 2006/140 **1 PT**

Kenya, SE-Aberdare, - 0°23`N/36°46`E, 2750 m, - 16.-21.II.1999 Th. Wagner leg. / Paratypus / Enochrus (Meth.) - perssoni sp. n. - det. F. HEBAUER

16.-21. Februay 1999

SE-Aberdare, Central, Kenya, Africa

0°23`N, 36°46`E (site information)

wagneri Hebauer, 2002b: 14 *(Helochares)*

COL 2006/139 **1 PT**

Kenya, Kakamega F. - 0°22`N/34°50`E, 1600 m, - 7-11.II.99, Th. Wagner leg. / Paratypus - Helochares - wagneri sp. n. - des. F. Hebauer

7.-11. Februay 1999

Kakamega Forest, Western, Kenya, Africa

0°17`N, 34°53`E (exact gathering site information; imprecise data on original label!)

LAEMOPHLOEIDAE

wagneri Karner, 1997: 95-98 *(Notolaemus)*

COL 2006/142 **♂ HT** **(Fig. 30)**

Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / T.n. 5 / Holotypus - Notolaemus - wagneri - n.sp. ♂ - M. Karner 1996

October 1993

Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa

2°15`S, 30°50`E (gathering site: estimated value)

COL 2006/143 **1 ♂ PT**

COL 2006/144-148 **5 ♀ PT**

October 1993

Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa

2°15`S, 30°50`E (gathering site: estimated value)

MELYRIDAE

adrastus Evers, 1998: 63-64 *(Sphinginopalpus)*

COL 2006/164 **♂ HT** **(Fig. 31)**

Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / T.n.8 / Von Teclea nobilis gefoggt / Holotypus ♂ / Sphinginopalpus - adrastus Evers - A. Evers det. 1997

October 1993

Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa

2°15`S, 30°50`E (gathering site: estimated value)

carapae Evers, 1998: 60-62 *(Attalus)*

COL 2006/149,151,153 **3 ♀ PT**

Rwanda, Nyungwe - Kamiranzovu, 2000 m - Th. Wagner leg. X.93 / C.g.2 / Von Carapa grandiflora gefoggt / Paratypus ♀ / Attalus - carapae Evers - A. Evers det. 1997

October 1993

Kamiranzovu, Nyungwe Forest, Cyangugu, Rwanda, Africa

2°29`S, 29°09`E (gathering site: estimated value)

COL 2006/150 **1 ♀ PT**

October 1993

Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa

2°33`S, 28°59`E (gathering site: estimated value)

COL 2006/152 **1 ♂ PT**

October 1993

Karengera, Cyangugu, Rwanda, Africa

2°31`S, 29°02`E (gathering site: estimated value)

karengerae Evers, 1998: 62 *(Attalus)*

COL 2006/154 **1 ♀ AT**

Rwanda, 1700 m - Karengera, X.93 - Th. Wagner leg. / C.g.1 1 / Von Carapa grandiflora gefoggt / Allotypus ♀ / Attalus - karengerae Evers - A. Evers det. 1997

October 1993

Karengera, Cyangugu, Rwanda, Africa

2°31`S, 29°02`E (gathering site: estimated value)

lateridentatus Evers, 1998: 64 *(Colotes)*

COL 2006/165 **♂ HT** **(Fig. 32)**

Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / T.n.6 / Von Teclea nobilis gefoggt / Holotypus ♂ / ♂ / Colotes lateridentatus Evers - A. Evers det. 1997

October 1993

Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa

2°15`S, 30°50`E (gathering site: estimated value)

COL 2006/166-170 **5 ♀ PT**

October 1993

Ibanda Makera, Rusumo, Cyangugu, Rwanda, Africa

2°15`S, 30°50`E (gathering site: estimated value)

stilifer Evers, 1998: 60 *(Afrocarphurus)*

COL 2006/163 **1 ♀ PT**

Rwanda, Karengera - Cyamudongo X.93 - Th. Wagner leg. / C.g.3 / Von Carapa grandiflora gefoggt / Paratypus ♀ / Afrocarphurus - stilifer Evers - A. Evers det.1997 / 1 Paratypus – ♀ behalten

October 1993

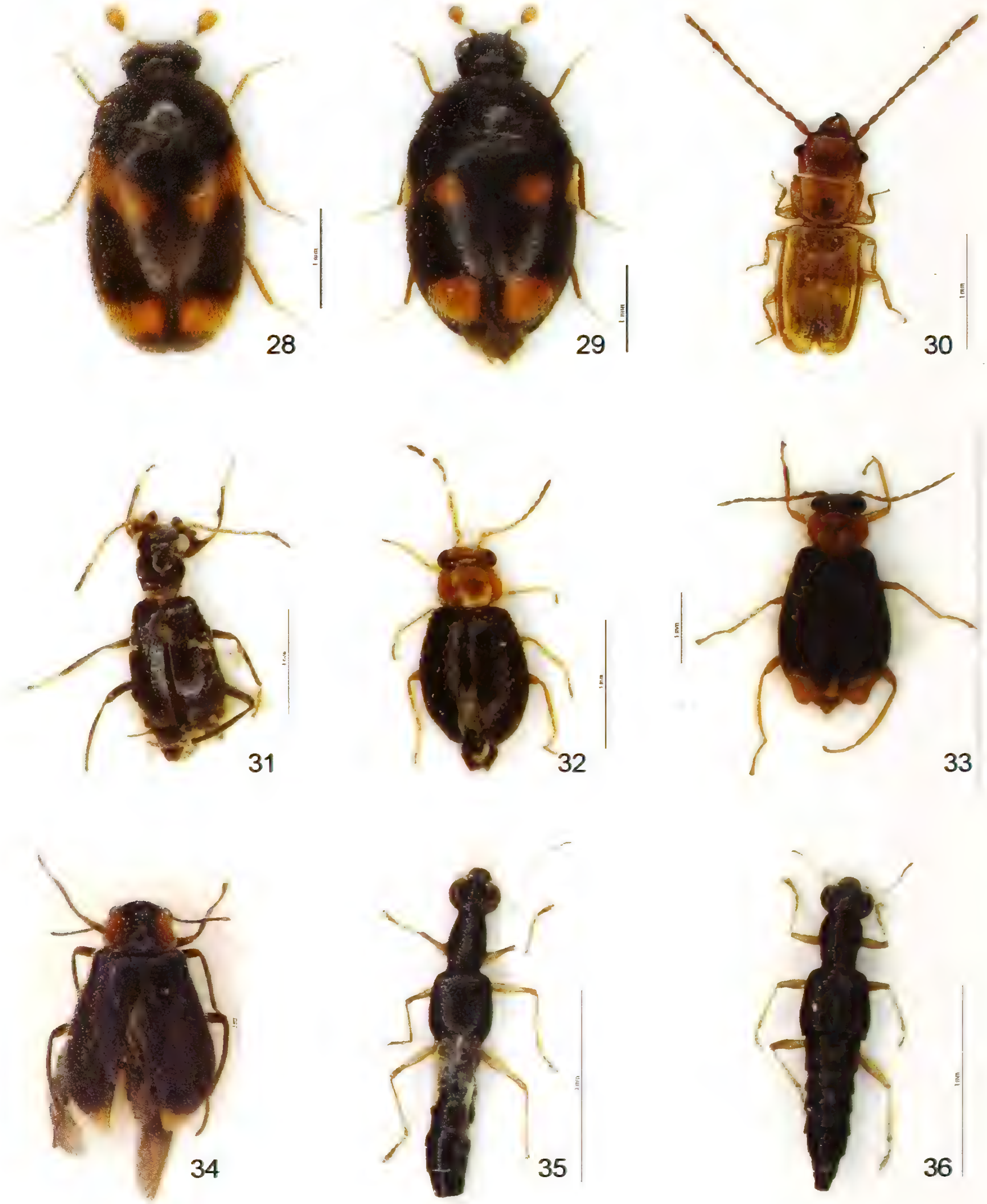
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa

2°33`S, 28°59`E (gathering site: estimated value)

tecleae Evers, 1998: 64-65 *(Morphotroglops)*

COL 2006/162 **1 ♀ AT**

Rwanda, Rusumo - Ibanda Makera, X.93 - Th. Wagner leg. / T.n.8 / Von Teclea nobilis gefoggt / Allotypus ♀ / Morphotroglops - tecleae Evers - A. Evers det.1997



Figs 28–36. *Orphinus rusumoensis* Háva & Herrmann, 2002 (**28**) ♂ HT, *Orphinus wagneri* Háva & Herrmann, 2002 (**29**) ♂ HT, *Notolaemus wagneri* Karner, 1997 (**30**) ♂ HT, *Sphinginopalpus adrastus* Evers, 1998 (**31**) ♂ HT, *Colotes lateridentatus* Evers, 1998 (**32**) ♂ HT, *Afroebaeus wagneri* Evers, 1998 (**33**) ♂ HT, *Attalus wagneri* Evers, 1998 (**34**) ♂ HT, *Stenus arborarius* Puthz, 1999 (**35**) ♂ HT, *Stenus wagnerianus* Puthz, 1999 (**36**) ♂ HT: Habitus in dorsal view.

October 1993
Ibanda Makera, Rusumo, Kibungo, Rwanda, Africa
2°15`S, 30°50`E (gathering site: estimated value)

wagneri Evers, 1998: 65 (*Afroebaeus)*

COL 2006/155 ♂ HT (Fig. 33)
Rwanda, Karengera - Cyamudongo X.93 - Th. Wagner leg. / C.g.4 / Von Carapa grandiflora gefoggt / Holotypus ♂ / Afroebaeus - wagneri Evers - A. Evers det. 1997
October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)

COL 2006/158,160 2 ♀ PT

COL 2006/159 1 ♂ PT
October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)

COL 2006/161 1 ♀ PT
October 1993
Cyamudongo, Nyakabuye, Cyangugu, Rwanda, Africa
2°33`S, 28°59`E (gathering site: estimated value)

wagneri Evers, 1998: 62-63 (*Attalus)*

COL 2006/156 ♀ HT (Fig. 34)
Rwanda, Karengera - Cyamudongo X.93 - Th. Wagner leg. / C.g.1 / Von Carapa grandiflora gefoggt / Holotypus ♀ / Attalus - wagneri Evers - A. Evers det. 1997
October 1993
Karengera, Cyangugu, Rwanda, Africa
2°31`S, 29°02`E (gathering site: estimated value)

COL 2006/157 1 ♀ PT
October 1993
Kamiranzovu, Nyungwe Forest, Cyangugu, Rwanda, Africa
2°29`S, 29°09`E (gathering site: estimated value)

STAPHYLINIDAE

arborarius Puthz, 1999a: 15-17 *(Stenus)*

COL 2006/171 ♂ HT (Fig. 35)
Uganda, District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`W 11.-20.VII.95 - Th. Wagner leg. / T.n.17 4 / Puthz, 1998 / Stenus - arborarius - spec. nov. - det. V. Puthz 1998 / 1 pt behalten
11.-20. July 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (exact gathering site information; error on original label!)

COL 2006/172 1 ♂ PT
15.-25. January 1997
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (gathering site)

wagneri Puthz, 1999b: 21 *(Megalopinus)*

COL 2007/279 ♀ HT (Fig. 36)
Uganda District Masindi - Budongo Forest n. Sonso - 1°45`N, 31°35`W 19.-30.VI.95 - Th. Wagner leg. / T.r.3 1 / Holotypus / Megalopinus - wagneri - spec. nov. - det. V. Puthz 1998
19.-30. June 1995
Sonso River (Budongo Forest), Masindi, Uganda, Africa
1°45`N, 31°35`E (exact gathering site information; error on original label!)

wagnerianus Puthz, 1999a: 18-19 *(Stenus)*

COL 2006/173 ♂ HT (Fig. 37)
Rwanda, Nyungwe - Kamiranzovu, 2000 m - Th. Wagner leg. X.93 / ♂ - Holotypus / Stenus - wagnerianus - spec. nov. - det. V. Puthz 1998 / 1 pt behalten
October 1993
Kamiranzovu, Nyungwe Forest, Cyangugu, Rwanda, Africa
2°29`S, 29°09`E (gathering site: estimated value)

COL 2006/174 1 ♂ PT
October 1993
Kamiranzovu, Nyungwe Forest, Cyangugu, Rwanda, Africa
2°29`S, 29°09`E (gathering site: estimated value)

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(see contribution of Marc G. M.VAN ROOSMALEN, pp. 105–112)

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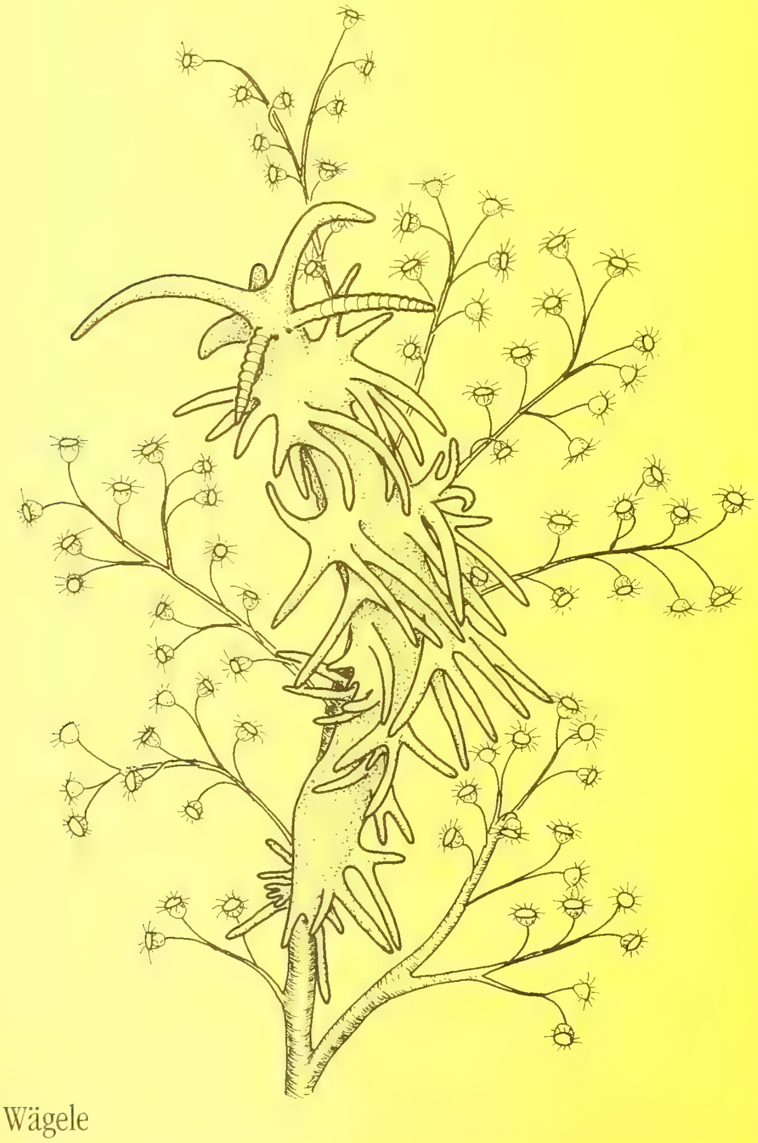

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Distribution of homarine in some Opisthobranchia (Gastropoda: Mollusca)*

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Abstract. Homarine, a zwitterionic natural product, is only known from some marine invertebrates, including the opisthobranch *Phestilla lugubris* (Klein 1986 in KARUSO 1987). This natural product is described as having antipredatory and antifouling effects. In the current study we present new results on the distribution of homarine in Opisthobranchia and in a few of their food organisms. Our results indicate that homarine is mainly found in members of the Cladobranchia (with one exception) and is probably derived from cnidarian food sources. Other investigated opisthobranch taxa, which feed on a variety of other marine organisms (algae, Porifera, Bryozoa etc.), lack homarine. An exception is the cephalaspid *Aglaja tricolorata* in which homarine was detected, and foraging of this predatory slug on homarine containing cladobranchs seems likely. It is shown in *Marionia blainvillea* that the characteristic glandular cells in the epidermis of the Dendronotoidea are not adaptations to store homarine.

Keywords. Natural products, Cnidaria, food organisms, Cladobranchia, *Marionia blainvillea*, histology.

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1. INTRODUCTION

A wide variety of natural products is known from Opisthobranchia (KARUSO 1987; AVILA 1995; CIMINO et al. 1999; CIMINO et al. 2001; CIMINO & GAVAGNIN 2006; WÄGELE et al. 2006). Some of the opisthobranchs are of particular interest due to their extreme toxicity and the high structural diversity of their secondary metabolite content.

One of these groups is the algae- or cyanobacteria-feeding taxon Anaspidea, which store a high diversity of secondary metabolites. Apart from terpenes, which are the major structural class in Anaspidea, bioactive polyketides and peptides were also found (CAREFOOT 1987; YAMADA & KIGOSHI 1997; CIMINO et al. 2001). One of these peptides, i.e. dolastatin 10, showed potent cytotoxic activity. In clinical studies (phase II), however it had no effect neither against advanced colorectal cancer (SAAD et al. 2002), advanced pancreaticobiliary cancers (KINDLER et al. 2005), nor advanced breast cancer (PEREZ et al. 2005).

The Sacoglossa, which mainly feed on algae of the taxon Chlorophyta, obtain secondary metabolites from their food. One of these compounds, the depsipeptide kahalalide F that *Elysia rufescens* takes up from its food alga *Bryopsis* spec. and algal associated bacteria is currently in a clinical trial (phase II) against hepatocellular carcinoma, non-small cell lung cancer and melanoma (HAMANN 2004). In some cases these sequestered chemicals are biotransformed by the slugs. Thus Mediterranean *Oxynoe olivacea, Lobiger serradifalci* and *Ascobulla fragilis*, all of which feeding on *Caulerpa prolifera*, take up the algal sesquiterpenoid caulerpenyne and modify it into oxytoxin-1 and -2, which have an enhanced deterrent effect against fish compared to caulerpenyne (CIMINO et al. 1990; GAVAGNIN et al. 1994a). According to CIMINO & GHISELIN (1998), CIMINO et al. (1999) and MARIN & ROS (2004) highly derived sacoglossans are able to form their defensive compounds *de novo*. E.g. GAVAGNIN et al. (1994b) showed that the polypropionate elysione is produced by *Elysia viridis* itself..

Within the Nudibranchia, the sponge-feeding Doridoidea are probably the group among the Opisthobranchia best examined for the presence of secondary metabolites, most of which are dietary derived terpenes (see e.g. the reviews KARUSO et al. 1987; AVILA 1995; CIMINO et al. 1999; GAVAGNIN & FONTANA 2000; GARSON 2006; WAHIDULLAH et al. 2006; MIYAMOTO 2006). *De novo* biosynthesis, however, has also been shown, e.g., for the sesquiterpenes polygodial in *Dendrodoris limbata* (Cimino et al. 1983) and *ent*-pallescensin A in *Doriopsilla areolata* (Gavagnin et al. 2001).

In contrast, the nudibranch taxon Cladobranchia has been poorly investigated chemically. Traditionially, Cladobranchia are divided into three taxa, the monophyletic Aeolidoidea and Dendronotoidea, and the paraphyletic Arminoidea (see Wägele & Willan 2000). Members of the Cladobranchia mainly feed on octocorals and hydrozoans (McDonald & Nybakken 1997). Within the Arminoidea few terpenes have been detected. The briarane diterpenoids verecynarmin A to G and the cembranoid preverecynarmin are known from *Armina maculata* and its prey organism, the octocoral *Veretillum cynomorium* (Guerriero et al. 1987, 1988, 1990). *Leminda millecra* exhibits four different sesquiterpenoids, millecrone A and B, as well as millecrol A and B (Cimino et al. 2001). They all are sequestered while feeding on alcyonariids. Further investigation revealed more natural compounds: isofuranodiene, (+)-8-hydroxycalamenene, algoafuran, cubebenone, and a series of seven triprenylquinones and hydroquinones. *Alcyonium fauri* and the gorgonian *Leptogorgia palma* seem to be the source of at least some of these compounds (McPhail et al. 2001). Origin of janolusimide, extracted from *Janolus cristatus* (Sodano & Spinella 1986) seems to be unknown, a *de novo* biosynthesis can not be excluded (Cimino et al. 2001).

Terpenes are also present in Dendronotoidea. *Tritonia hamnerorum* e.g. sequesters the feeding deterrent sesquiterpene julieannafuran from its food, which is the sea fan *Gorgonia ventalina* (Cronin et al. 1995). Several terpenes (rubifolide, pukalide, cuparane sesquiterpenoides) and other compounds (tochuinyl acetate and its dihydro-derivative, ptilosarcenone) are collected from *Tochuina tetraquetra*. All these products seem to be food derived (Cimino et al. 2001). Further compounds in other members of Dendronotoidea are summarized by Cimino et al. (2001): An unknown *Tritonia* sp. revealed a prostanoid, also found in the octocoral *Telesto*, and *Tritoniella belli* sequestered a chimyl alcohol from the octocoral *Clavularia frankliniana*. *De novo* biosynthesis of terpenes is recorded from one member of the Dendronotoidea: Barsby et al. (2002) showed through feeding experiments with [1,2-$^{13}C_2$] acetate that *Melibe leonina* produces at least one of its defensive metabolites (2,6-dimethyl-5-heptenal) itself.

In the Aeolidoidea terpenes are only known from the genus *Phyllodesmium*. *P. longicirrum* accumulates three cembranoid diterpenes, trocheliophorol, thunbergol and epoxythunbergol, from the soft coral *Sarcophyton trocheliophorum* (Coll et al. 1985). *P. guamensis* specifically sequesters the cembranoid 11-beta-acetoxypukalide from its preferred prey, the soft coral *Sinularia maxima* (Slattery et al. 1998). Only very few records for other compounds are available. Ciavatta et al. (1996) discovered two prenylchromanols (1 and 2) and a prenyl-p-hydroxy acid in the skin of *Cratena peregrina*. None of these compounds was detected in the preferred food of *C. peregrina*, namely the hydrozoan *Eudendrium racemosum*. On the other hand, other metabolites, usually not considered as deterrent to predators have been isolated from *Eudendrium* and its aeolid predators: carotenoids from *Flabellina iodinea* (McBeth 1972), sterols from *Cratena peregrina*, *Flabellina affinis* and *F. lineolata* (Cimino et al. 1980), carotenoids and alkaloids from *Phestilla melanobrachia* (Okuda et al. 1982), sterols and alkaloids from *P. lugubris* (Targett 1983; Karuso 1987). Karuso (1987, after Klein 1986) reported also the presence of homarine in the latter species.

Members of the Aeolidoidea are known for storing cnidocysts from their prey organisms in special structures located at the cerata tips (see Fig. 1A). Here, a cnidosac is formed as part of the digestive gland, and in the cells of this sac, intact cnidocysts are incorporated and maintained functional. It is assumed that the slugs use these cnidosysts as a major means of defense (e.g. Edmunds 1966; Greenwood & Mariscal 1984a, b). This assumption is supported by the studies of Frick (2003), showing that *Flabellina verrucosa* responds to the presence of predators by the variation of nematocyst incorporation.

The incorporation of cnidocysts is regarded as the main key character in the evolution of the Aeolidoidea (Wägele 2004). Nevertheless, in some cases secondary metabolites seem to be of importance for aeolids as well, e.g. in the genus *Phyllodesmium* where no incorporation of cnidocysts takes place (Slattery et al. 1998). The same holds true for *Phestilla lugubris*, which shows no cnidocysts in their cnidosacs, but homarine was found (Karuso 1987, after Klein 1986).

Homarine was first isolated in 1933 by Hoppe-Seyler. Its biological function has been controversially discussed ever since. This product seems to be restricted to marine organisms, and within the Metazoa it is only found in invertebrates (Carr et al. 1996). Therefore it was suspected that its purpose lies in osmoregulation. Beers (1967) studied the distribution of homarine in Crustacea, Echinodermata and Tunicata and from these results infered that the presence of homarine is "in basic accord with a role in cellular osmotic phenomena". Dall (1971) though could not find any contribution of homarine in osmotic processes in decapod crustaceans. Nevertheless, it is widely accepted that homarine serves as an osmolyte in marine algae. Initial studies have been carried out by Dickson & Kirst (1986) with the green alga *Platymonas sub-*

cordiformis. Slattery et al. (1997) showed that the soft coral *Gersemia antarctica* releases a potent antimicrobial mixture of organic compounds into the surrounding seawater, and homarine is the compound responsible for most of this biological activity. In the tissues of the anthozoans *Actinia equina* and *Calliactis parasitica,* homarine was detected at concentrations of 1.5 and 2.1 mg/g dry weight (Mathias et al. 1960). Berking (1986, 1987) detected homarine in several hydrozoans, where it regulates the colony morphology and prevents the metamorphosis in larvae. Detection of homarine in gastropods is rare. McClintock (1994) found the substance in the Antarctic *Marseniopsis mollis* (Caenogastropoda, Marseniidae). It is probably derived from epizoic bryozoans and hydrozoans growing on the ascidian *Cnemidocarpa verrucosa*, the main food of *M. mollis* and serves as a feeding deterrent against the seastar *Odontaster validus*.

Since homarine was found in aeolids without cnidocysts, the question arouse, whether the occurence of homarine with a possible defensive function is more widespread in opisthobranchs.The current study focuses on the distribution of homarine in several opisthobranch taxa, with a main focus on Cladobranchia, since this group is hardly investigated concerning its chemical defensive systems. Furthermore the localisation of this compound within the body of the dendronotoid *Marionia blainvillea* (Fig. 1B) was investigated in detail. The epidermal tissue of the mantle of *M. blainvillea* is densely packed with glands of unknown function (Wägele et al. 2006) (Fig. 1C). Therefore a role of these glands in chemical defense was considered likely.

2. MATERIAL AND METHODS

Specimens of the opisthobranchs and of their food were collected worldwide during several field trips. Table 1 lists the investigated specimens, the collection details, and the means of extraction. The animals were fixated either in alcohol (ethanol or methanol) or by deep freezing.

The supernatant alcohol was taken off and used for the preparation of a crude extract, or in the case of the deep frozen samples extraction with methanol was carried out. The solvent was evaporated under reduced pressure with a rotary evaporator in order to obtain a crude extract.

The detection of homarine was carried out via ^{1}H NMR spectroscopy on a Bruker Avance 300 DPX spectrometer, using D_2O as solvent.

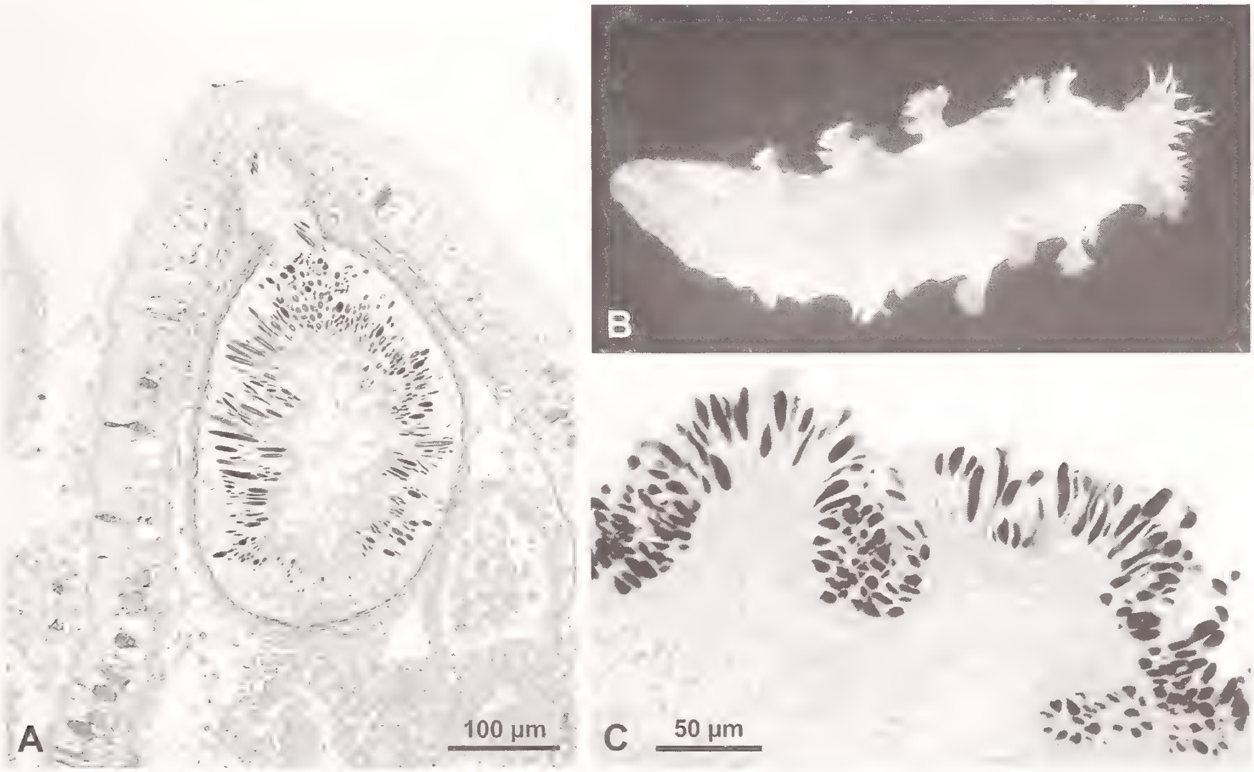

Fig. 1. A. typical cnidosac (here *Aeolidia papillosa*). B. *Marionia blainvillea* C. Histological section of dorsal mantle epithelium of *Marionia blainvillea.* Note the single vacuoles in the cells staining homogenously dark violet.

Table 1. Species investigated for homarine, with information on location, date of collection, extraction type and result. Food organism or substrate is indicated in the last column. These information are taken from McDonald & Nybakken (1997) if not stated otherwise. + homarine present; – no signal of homarine present in ^{1}H NMR and total amount of crude extract >100mg; ? insufficient amount of crude extract (<10mg); Column 5 (Extraction): fluid in brackets indicate that only the alcohol for fixation was used for the preparation of a crude extract

Higher ranking Taxon/*Species*	Location	Number of Indiv. Date of collection	Fixation	Extraction	Homarine	Food
		Opisthobranchia				
Aeolidoidea						
Cratena pilata (Gould, 1870)	Blanes, Spain	04.11.1993	Deep frozen	MeOH	+	*Tubularia* spp., and other hydrozoans
Cuthona caerulea (Montagu, 1840)	Banyuls-sur-Mer, France	05.2006	EtOH	(EtOH)	+	diverse hydrozoan species
Cuthona gymnota (Couthouy, 1838)	Blanes, Spain	04.11.1993	Deep frozen	MeOH	+	*Tubularia* spp., and other hydrozoans
Flabellina affinis (Gmelin, 1791)	Banyuls-sur-Mer, France	05.2006	EtOH	(EtOH)	?	*Eudendrium* spp.
Hermissenda crassicornis (Eschscholtz, 1831)	Blanes, Spain	5 Indiv. 24.03.1994	Deep frozen	MeOH	+	Examined specimens found on *Tubularia crocea*, also on diverse hydrozoans
Phestilla lugubris (Bergh, 1870)	Data taken from Karuso 1987 (after Klein 1986)				+	*Porites* spp.
Phyllodesmium spec.	Lizard Island, Australia	14.07.2006	MeOH	(MeOH)	–	Specialised on Xeniidae. (pers. obs. HW)
Dendronotoidea						
Marionia blainvillea (Risso, 1818)	Blanes, Spain	5 Indiv. 09.2004	Deep frozen	MeOH	+	e.g. *Eunicella singularis*, also on other gorgonians
Marionia blainvillea (Risso, 1818)	Blanes, Spain	10 Indiv. 05.2006	EtOH	(EtOH)	–	
Tritonia striata Haefelfinger, 1963	Blanes, Spain	15 Indiv. 04.–07.2004	Deep frozen	MeOH	?	*Paralcyonium elegans* (see Schmekel & Portmann 1982)
Tritonia manicata Deshayes, 1853	Blanes, Spain	11 Indiv. 03.–08.2004	Deep frozen	MeOH	?	*Clavularia* sp., *Cornularia* spp. (Alcynonacea)
Doridoidea						
Dendrodoris grandiflora Rapp, 1827	Tierra de Malgrat, Spain	05.11.2004	EtOH 96%	(EtOH)	–	Sponges e.g. *Ircinia fasciculata, Clathria toxystila, Spongia officinalis*
Platydoris argo (Linné, 1767)	Giglio, Italy	05.2005	EtOH 70%	(EtOH)	–	Demospongia
Adalaria proxima (Alder & Hancock, 1854)	Bretagne, France	07.1996	EtOH 93%	(EtOH)	–	Bryozoa
Archidoris pseudoargus (Rapp, 1827)	Tierra de Malgrat, Spain	05.11.2004	EtOH 96%	(EtOH)	–	Demospongia
Cephalaspidea						
Scaphander lignarius (Linné, 1758)	Blanes, Spain	5 Indiv. 11.11.2004	EtOH 70%	(EtOH)		Predatory e.g. Polychaeta
Aglaja tricolorata Renier, 1807	Giglio, Italy	05.2005	EtOH 70%	(EtOH)	+	Predatory, other Opisthobranchia
Anaspidea						
Aplysia spec.	La Coruña, Spain	08.03.2006	EtOH 96%	(EtOH)	–	Algae
Phyllaplysia spec.	Banyuls-sur-Mer, France	09.1994	EtOH	(EtOH)	–	Algae

Higher ranking Taxon/*Species*	Location	Number of Indiv. Date of collection	Fixation	Extraction	Homarine	Food
Pleurobranchoidea						
Bathyberthella antarctica Willan & Bertsch, 1987	Antarctica 61°43,30'S 59°12,40'W	27.11.1996	EtOH 70%	(EtOH)	–	unknown
Tylodinoidea						
Umbraculum umbraculum (Lightfoot, 1786)	Meteor Bank ST 486 (N-Atlantic) 29°45,7' N 28°22.9' W	08.09.1998	EtOH 80%	(EtOH)	–	Demospongia
		Other gastropods				
„Prosobranchia"						
Littorina littorea Linné, 1758	Nordstrand, Germany	10 Indiv. 22.08.2006	EtOH 98%	(EtOH)	–	
		Food of the examined Opisthobranchia				
Octocorallia						
Eunicella singularis (Esper, 1791)	Banyuls-sur-Mer, France	05.2006	EtOH 98%	(EtOH)	+	
Xenniidae	Lizard Island, Australia	14.07.2006	MeOH	(MeOH)	–	
Hydrozoa						
Tubularia crocea Agassiz, 1862	Blanes, Spain	04.11.1993	Deep frozen	MeOH	+	

From 1 g of the crude extract of one colony of the gorgonian *Eunicella singularis* 4 mg of homarine were isolated by RP-18 VLC and HPLC. The VLC was carried out using a 2.5 cm glass column filled 10 cm with Silica gel Polygoprep 60-50 C18. Elution was performed using a water/methanol gradient starting with pure water, yielding 13 fractions.

The HPLC was performed on a Shimadzu system equipped with a Merk Hitachi Pump L-7100 and a Shimadzu SPD-M6A Photodiode Array UV-VIS detector, using a Knauer C_{18} Eurospher-100 (5 µm, 250x80 mm) column. A constant flow of 1 mL/sec was applied using Water/Methanol (90:10 V/V) as eluent.

The five deep frozen specimens of *Marionia blainvillea* were dissected before extraction into mantle, foot, digestive gland and the rest of the viscera, in order to examine the distribution of homarine within the body of the animal.

For histological investigation, one specimen each of the dendronotoid *Mariona blainvillea* and the aeolid *Cuthona caerulea* have been preserved in formaldehyde/seawater. After dehydration in alcohol, they were embedded in hydroxyethylmethacrylate for serial sectioning and sections (2.5 µm) were stained with toluidine blue. Investigation was performed under a light microscope.

3. RESULTS

The survey of several members of the Opisthobranchia revealed that the natural compound homarine is present in all examined samples of Cladobranchia, apart from a new species of *Phyllodesmium* from Lizard Island. This compound was also not found in other members of the Opisthobranchia, except for *Aglaja tricolorata.* Results of this survey are listed in Table 1.

The low field shifted ^{1}H NMR signals of homarine δ 7.8 – 8.9 ppm (see Fig. 2) are very characteristic for this compound, and can easily be detected in ^{1}H NMR spectra of crude extracts. In all cases they did not overlap with any other resonance signals. The detection of these resonance signals is a clear indication for the presence of homarine, however only if the concentration of the compound is sufficient, i.e. traces will not be detected.

For specific localisation of the compound different body parts of *M. blainvillea* were extracted separately. ^{1}H NMR spectra of the extracts show that homarine is present throughout the body (see Fig. 3 A to D).

Histological investigation revealed that the epidermis of *M. blainvillea* contains many epithelial glandular cells with one large vacuole filling the whole cell. The vacuole contains a substance that is stained homogeneously dark violett with toluidine blue (Fig. 1C). These glandular cells are evenly distributed over the dorsal and lateral notum.

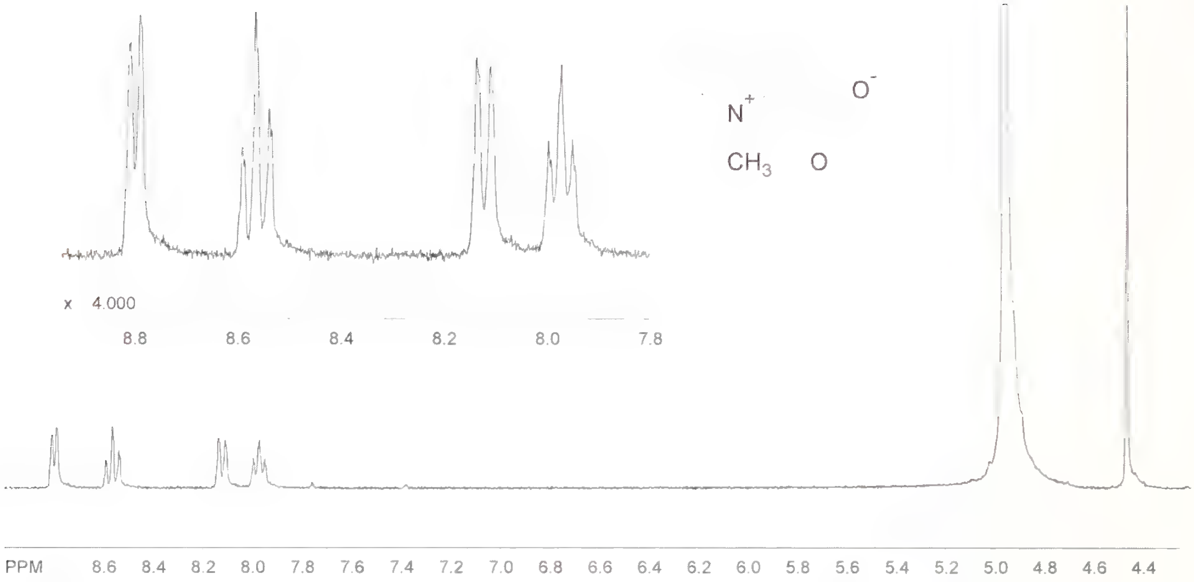

Fig. 2. ^{1}H NMR spectrum of purified homarine in methanol-d$_4$. 300 MHz, and chemical structure of homarine.

The epithelium of *Cuthona caerulea* showed very few glandular cells, these were usually filled with dark staining granular substances.

4. DISCUSSION

Secondary metabolites clearly seem to play a role in the biotic interactions with potential predators throughout all systematic groups of Opisthobranchia. These chemicals are often taken up from the food while *de novo* synthesis is rare (review see Cimino et al. 2004).

Only a few field studies on the deterrent effect of the observed compounds have been carried out (Thompson 1960; Avila & Paul 1997; Slattery et al. 1998; Johnson & Willows 1999; Marin et al. 1999; Avila et al. 2000; Becerro et al. 2001; Iken et al. 2002; Rogers et al. 2002; Penney 2004). While even a few studies focus on parasites on opisthobranchs (Arnaud 1978; Ho 1981; Carefoot 1987; Jensen 1987; Huys 2001; Schrödl 2002, 2003), the effect of secondary metabolites on pathogens is hardly investigated. Teeyapant et al. (1993a, b) studied the uptake of secondary metabolites in *Tylodina perversa* (Tylodinoidea) from its food sponge *Aplysina* (*Verongia*) *aerophoba* and the antimicrobial activity of the sponge metabolites. However they only found antimicrobial activity in compounds that were not present in *Tylodina perversa*.

Incorporation of homarine is shown here for slugs feeding on Hydrozoa as well as on the gorgonian octocoral *E. singularis*. The examined Hydrozoa contained homarine, which is in accord with its role as a morphogen, supposedly in all hydrozoans (Berking 1986, 1987). The examined gorgonian *E. singularis* also contained homarine as described for other gorgonians where it serves as an antifouling agent (Targett et al. 1983). Uptake of homarine can also occur by predation on opisthobranchs containing homarine. According to Rudman (1972), members of the genus *Aglaja* are active predators, feeding on vagile prey. Whereas some aglajid species, like *A. cylindrica*, specialize on polychaetes and nemertines, others (e.g. *A. aureopunctata*) mainly focus on opisthobranchs. It seems likely that *Aglaja tricolorata* obtained the homarine by feeding on other opisthobranchs.

Several of the investigated species belong to the Aeolidoidea with functional cnidocysts incorporated, which are a good means of defense against predatory fishes (Frick 2003) but certainly useless against crustaceans and probably without effect against seastars. Both latter groups are potential predators on opisthobranchs, though only few thorough investigations on predation have been carried out (review see Wägele et al. 2006). The efficiency of homarine as a feeding deterrent is shown e.g. in *Marseniopsis mollis* (McClintock 1994). But similar studies have never been performed for opisthobranchs and further investigations are needed to clarify the role of this compound in cladobranchs. The presence of a further defensive system, like homarine, would provide additional protection, e.g. for the cnidocyst containing *Cuthona caerulea*. In species without cnidocysts, e.g. *Marionia blainvillea*, homarine might even represent the sole defensive strategy.

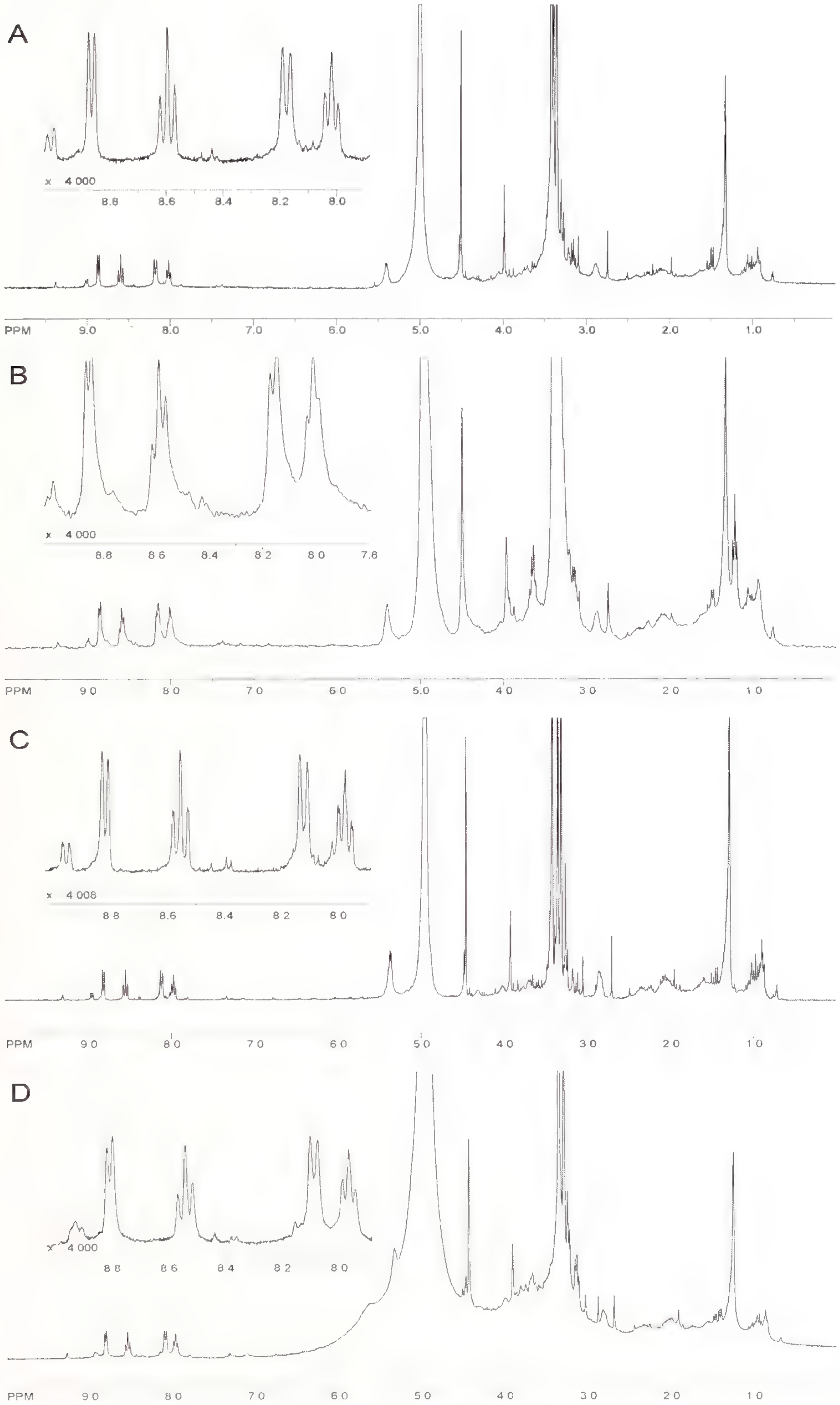

Fig. 3. ^{1}H NMR spectra of crude extracts of dissected *Marionia blainvillea* in methanol-d_4. 300 MHz. A. Mantle, B. Foot, C. Digestive gland, D. Viscera without digestive gland.

Homarine could also serve as an antibacterial agent in the mucus layer of the slugs, independent of its supposed function as a feeding deterrent, since any kind of mucus is a perfect environment for bacteria or fungi. Therefore, organisms with a mucus layer can adopt two ways of keeping their body surface clean. They can either produce big amounts of mucus that wash off continuously or add a substance that inhibits growth of microorganisms. The former strategy is known, e.g. from certain soft corals (Ducklow & Mitchell 1979; Duerden 1986), the latter could be the case in the Aeolidoidea and Dendronotoidea.

Wägele et al. (2006) noted the presence of homogenously staining violet glands as a characteristic of Dendronotoidea. In their survey on glandular structures in Opisthobranchia, they observed these glands for nine (out of 17 investigated) members of the Dendronotoidea. These glands are absent in any members of the Aeolidoidea and "Arminoidea". We confirmed the presence of these particular glands in *Marionia blainvillea* and their absence in *Cuthona caerulea*. The uniform distribution of homarine in the different body parts of *M. blainvillea* suggests that no bioaccumulation in the glandular epithelium takes place in this case. Homarine is a very small and very polar molecule, therefore it is likely that it is taken up passively in the digestive gland or even in the whole digestive system. Quantitative analyses still should be carried out to support this supposition. Since homarine is also present in *C. caerulea*, we can conclude that these particular epidermal glandular structures of the Dendronotoidea are not a morphological adaptation to store homarine. Their function remains unclear.

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Utility of H3-Genesequences for phylogenetic reconstruction – a case study of heterobranch Gastropoda –*

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Abstract. In the present study we assessed the utility of H3-Genesequences for phylogenetic reconstruction of the Heterobranchia (Mollusca, Gastropoda). Therefore histone H3 data were collected for 49 species including most of the major groups. The sequence alignment provided a total of 246 sites of which 105 were variable and 96 parsimony informative. Twenty-four (of 82) first base positions were variable as were 78 of the third base positions but only 3 of the second base positions.

H3 analyses showed a high codon usage bias. The consistency index was low (0,210) and a substitution saturation was observed in the 3rd codon position. The alignment with the translation of the H3 DNA sequences to amino-acid sequences had no sites that were parsimony-informative within the Heterobranchia.

Phylogenetic trees were reconstructed using maximum parsimony, maximum likelihood and Bayesian methodologies. *Nodilittorina unifasciata* was used as outgroup.

The resolution of the deeper nodes was limited in this molecular study. The data themselves were not sufficient to clarify phylogenetic relationships within Heterobranchia. Neither the monophyly of the Euthyneura nor a step-by-step evolution by the "basal" groups was supported. A conclusion about the monophyly of Opisthobranchia and Pulmonata could not be extracted from our data because we did not have any resolution at this point.

We believe histone H3 alone provides no new marker for studying deep molecular evolution of the Heterobranchia due to the high grade of conservation and the low phylogenetic signal.

Surprisingly there was a good resolution on the genera level. Analyses conducted with maximum parsimony and Bayesian inference (using all data) recovered all (or nearly all) genera mostly with statistically significantly supported nodes. Further studies focusing on the possible utility of histone H3 for the resolution of recent splits will be necessary.

Keywords. Heterobranchia, Opisthobranchia, histone H3, molecular phylogeny.

1. INTRODUCTION

Many questions regarding gastropod phylogeny have not yet been answered such as the molecular confirmation of the Heterobranchia concept based on morphological studies from HASZPRUNAR (1985, 1988). This taxon contains the Pentaganglionata HASZPRUNAR, 1985 also known as Euthyneura SPENGEL, 1881 (with the Opisthobranchia and Pulmonata) and several mostly little known "basal" groups (e.g. Valvatoidea, Omalogyroidea, Architectonicoidea, Rissoelloidea and Pyramidelloidea) which present a step-by-step evolution towards the euthyneuran level of organisation (HASZPRUNAR 1988). The hyperstrophy of the protoconch is the most important autapomorphous character of the Heterobranchia. The Euthyneura are characterised by the presence of two additional (so-called parietal) ganglia. However, the monophyly of the Euthyneura has not been clarified by molecular studies, yet. In some studies they are recovered monophyletic (COLGAN et al. 2000, 2003; KNUDSEN et al. 2006) in others not (THOLLESSON 1999). The Pulmonata and Opisthobranchia can be separated by characters respective of the nervous system (presence of a procerebrum and cerebral bodies in pulmonates and presence of a rhinophoral nerve in Opisthobranchia and Pyramidelloidea). However the molecular confirmation regarding the monophyly of the Opisthobranchia (VONNEMANN et al. 2005; GRANDE et al. 2004a) and the Pulmonata (TILLIER et al. 1996, DAYRAT et al. 2001) is still a matter of debate. There is no comprehensive investigation concerning the "basal" groups. Only a few representative taxa (e.g. Valvatoidea – *Cornirostra pellucida*, Architectonicoidea – *Philippea lutea*, Pyramidelloidea – *Pyramidella dolabrata*) have been included in current molecular studies (COLGAN et al. 2000; GRANDE et al. 2004a, 2004b).

In recent years molecular systematic analyses in gastropods have utilised a variety of genetic markers, e.g. nuclear 28S ribosomal RNA and/or 18S ribosomal RNA or mitochondrial 16S ribosomal RNA and/or cytochrome oxidase subunit I (Tillier et al. 1994, 1996; Dayrat et al. 2001; Vonnemann et al. 2005; Thollesson et al. 1999; Remigio & Hebert 2003). Nevertheless, new genetic markers are needed for the resolution of certain phylogenetic relationships (especially regarding deeper nodes). Partial fragments of the gene coding for the extremely conservative H3 protein (Maxson et al. 1983) were first used to clarify arthropod molecular evolution (Colgan et al. 1998) and later polychaete (Brown et al. 1999), gastropod (Colgan et al. 2000, 2003), polyplacophoran (Okusu et al. 2003), cephalopod (Lindgren et al. 2004) and hexapod (Kjer et al. 2006) phylogeny. All studies used a combined dataset in their approaches. In their study of gastropod phylogeny, Colgan et al. (2000) did not find a monophyletic Heterobranchia while within the Euthyneura, the Opisthobranchia are paraphyletic with respect to the pulmonates. Very similar phylogenetic relationships were shown in Colgan et al. (2003). The Heterobranchia as well as the Opisthobranchia and Pulmonata are rarely recovered as monophyletic in these studies.

In the present study we wanted to test the utility of H3 gene sequences for phylogenetic reconstruction within the Heterobranchia (focusing primarily on the Opisthobranchia). We were especially interested in testing whether H3 is suitable to resolve deeper nodes within heterobranch phylogeny. Therefore, partial histone H3 data were collected for 49 species including most of the major groups (Euthyneura with Opisthobranchia and Pulmonata and "basal" groups with Valvatoidea, Architectonicoidea, Omalogyroidea, Rissoelloidea and Pyramidelloidea).

2. MATERIALS AND METHODS

2.1. Specimens and DNA extraction

The studied taxa and the accession numbers are listed in Table 1. Twenty of the 49 sequences are taken from GenBank. Opisthobranchia are represented by 26 species (including 11 suborders). *Nodilittorina unifasciata* (Caenogastropoda Cox, 1960) was used as an outgroup.

DNA was extracted from ethanol-preserved individuals using the DNeasy Tissue Kit from Qiagen (Hilden, Germany).

Table 1 . Taxonomic positions and collecting locations of the sampled taxa. Accession numbers of sequences included in the analyses (ZSM = Zoologische Staatssammlung); published sequences taken from GenBank are marked with an asterisk.

Major Taxon	Species	Locality	GenBank Accession Number
Caenogastropoda			
Littorinoidea			
Littorinidae	*Nodilittorina unifasciata* (Gray, 1826)	Genbank	AF033705*
Conidae	*Conus miles* Linnaeus, 1758	Genbank	AF033684*
Campanilidae	*Campanile symbolicum* Iredale, 1917	Genbank	AF033683*
Opisthobranchia			
Nudibranchia			
Tethydidae	*Tethys fimbria* Linné, 1767	Blanes, Spain	EF133468
Discodorididae	*Discodoris atromaculata* (Bergh, 1880)	Genbank	DQ280013*
Arminidae	*Armina neapolitana* (Delle Chiaje, 1824)	Banyuls-sur-Mer, France	EF133469
Pleurobranchoidea			
Pleurobranchidae	*Pleurobranchaea meckeli* Leue, 1813	Blanes, Spain	EF133470
Tylodinoidea			
Umbraculidae	*Umbraculum umbraculum* (Lightfoot, 1786)	Atlantic Ocean, Meteor Bank	EF133471
Cephalaspidea			
Scaphandridae	*Scaphander lignarius* (Linné, 1758)	Blanes, Spain	EF133472
Philinidae	*Philine aperta* (Linnaeus, 1767)	Genbank	DQ093508*
Gastropteridae	*Gastropteron meckeli* Kosse, 1813	Blanes, Spain	EF133473
Anaspidea			
Akeridae	*Akera bullata* Müller, 1776	Kattegat, Denmark	EF133474
Aplysiidae	*Aplysia californica* Cooper, 1863	Miami, USA	EF133475
Aplysiidae	*Aplysia cf. juliana* Quoy & Gaimard, 1832	Genbank	AF033675*
Aplysiidae	*Bursatella leachii* de Blainville, 1817	Dingo Beach, Australia	EF133476
Thecosomata			
Cavoliniidae	*Clio pyramidata* Linné, 1767	Canary Islands; Spain	EF133477
Creseidae	*Creseis* sp.	Genbank	DQ280012*
Gymnosomata			
Pneumodermatidae	*Pneumoderma cf. atlantica* (Oken, 1815)	USA, Atlantic	EF133478

Major Taxon	Species	Locality	GenBank Accession Number
Sacoglossa			
Placobranchidae	*Elysia timida* (Risso, 1818)	Blanes, Spain	EF133479
Placobranchidae	*Elysia pusilla* (Bergh, 1872)	Genbank	DQ534792*
Placobranchidae	*Elysia crispata* Morch, 1863	Genbank	DQ534790*
Placobranchidae	*Elysia viridis* (Montagu, 1804)	Genbank	DQ534790*
Cylindrobullidae	*Cylindrobulla beauii* Fischer, 1857	Florida, USA	EF133480
Acochlidia			
Hedylopsidae	*Hedylopsis spiculifera* (Kowalewsky, 1901)	Rovinj, Croatia	EF133481
Microhedylidae	*Unela glandulifera* (Kowalewsky, 1901)	Rovinj, Croatia	EF133482
Architectibranchia			
Hydatinidae	*Micromelo undatus* (Bruguiere, 1792)	Genbank	DQ093513*
Acteonoidea			
Acteonidae	*Pupa solidula* (Linné, 1758)	Dingo Beach, Australia	EF133483
Acteonidae	*Rictaxis punctocaelatus* (Carpenter, 1864)	Cayucos, Californica, USA	EF133484
Bullinidae	*Bullina lineata* (Gray, 1825)	Genbank	AF033680*
Pulmonata			
Systellommatophora			
Onchidiidae	*Onchidium sp.*	Genbank	AF033706*
Onchidiidae	*Onchidella floridana* (Dall, 1885)	Florida, USA	EF133485
Onchidiidae	*Onchidella* sp.	Genbank	DQ093511*
Stylommatophora			
Charopidae	*Hedleyoconcha delta* (Pfeiffer, 1857)	Genbank	AF033693*
Siphonariidae	*Siphonaria serrata* (Fischer, 1807)	South Africa	EF133486
Siphonariidae	*Siphonaria concinna* Sowerby,1824	South Africa	EF133487
Siphonariidae	*Siphonaria zelandica* (Quoy & Gaimard, 1832)	Genbank	AF033713*
Amphibolidae	*Salinator solida* (Schacko, 1878)	Genbank	AF033712*
Eupulmonata			
Ellobiidae	*Ophicardelus ornatus* (Ferussac, 1821)	Genbank	AF033707*
“basal” Heterobranchia/Triganglionata			
Pyramidelloidea			
Pyramidellidae	*Turbonilla lactea* (Linné, 1758)	Roscoff, France	EF133488
Pyramidellidae	*Turbonilla sp.*	Wellington, New Zealand	EF133489
Architectonicoidea			
Architectonicidae	*Heliacus variegatus* (Gmelin, 1791)	Tropical aquarium (ZSM 20012193)	EF133490
Architectonicidae	*Philippea lutea* (Lamarck, 1822)	Genbank	AF033708*
Valvatoidea			
Cornirostridae	*Cornirostra pellucida* (Laseron, 1954)	Genbank	AF033685*
Orbitestellidae	*Orbitestella vera* Powell, 1940	Wellington, New Zealand	EF561623
Orbitestellidae	*Orbitestella* sp.	Leigh, New Zealand	EF561624
Omalogyroidea			
Omalogyridae	*Omalogyra burdwoodiana* Strebel, 1908	Antarctic (ZSM Mol-20021228)	EF133491
Rissoelloidea			
Rissoelidae	*Rissoella elongatospira* Ponder, 1966	Wellington, New Zealand	EF561622
Rissoelidae	*Rissoella micra* Finlay, 1924	Wellington, New Zealand	EF561620
Rissoelidae	*Rissoella cystophora* Finlay, 1924	Wellington, New Zealand	EF561621

2.2. DNA amplification and sequencing

The following degenerated primers were used: H3-F: 5’-ATG GCT CGT ACC AAG CAG AC(ACG) GC-3’ and H3-R: 5’-ATA TCC TT(AG) GGC AT(AG) AT(AG) GTG AC-3’ (Colgan et al. 1998) and produced a 246 bp product. The PCR profile was as follows: 95 °C for 5 min, followed by 35 cycles of 30 s at 95 °C, 25 s at 52 °C, 45 s at 72 °C and a final extension at 72 °C for 5 min and Taq Polymerase, recombinant from Invitrogen (Karlsruhe, Germany) was used. All products were purified using the QIAquick Gel Extraction Kit from Qiagen (Hilden, Germany) and sequenced in both directions with a CEQ 2000 Beckmann Coulter using the CEQ DTCS Quick Start Kit (Krefeld, Germany). First we sequenced only one fragment per specimen. Moreover, to avoid mistakes according to the conservative character of the H3 gene, we sequenced a random sample of 5 species a second time whereby no varieties could be detected.

2.3. Sequence alignment

Sequences were aligned manually using the software package BioEdit version 7.0.5 (Hall 1999). The H3 DNA sequences were translated into the amino acid sequences in GeneDoc version 2.6.002 (Nicholas & Nicholas 1997). The alignment is available from the authors upon request.

2.4. Statistical tests

Codon usage statistics were calculated using GCUA version 1.2 (McInerney 1997). The purpose of this function is to calculate the Number (N) of times a particular codon is observed in an alignment and also to calculate the Relative Synonymous Codon Usage (RSCU) values for the dataset. RSCU values define the number of times a particular codon is observed relative to the number of times that the codon would be observed in the absence of any codon usage bias. Without any codon usage bias, the RSCU value would be 1.00. A codon that is used less frequently than expected will have a value of less than 1.00 and a codon that is used more frequently than expected will have a volume of more than 1.00 (McInerney 1997).

The degree of bias ($\sum\chi^2/n$) which is the sum of the χ^2 values for the individual amino acids divided by the total number of inferred residues (n) for the combination of data from all species (Shields et al. 1988) was determined.

The substitution saturation was calculated for all 3 codon positions using the method developed by Xia et al. (2003) implemented in the software package DAMBE version 4.2.13 (Xia & Xie 2001).

2.5. Phylogenetic reconstruction

Appropriate models for the analyses were selected after running Modeltest version 3.4 (Posada & Crandall 1998) and using the Akaike information criterion (AIC) (see tab. 2).

The following analyses were conducted using PAUP* version 4.0 b10 (Swofford, 2002) (settings: heuristic search strategy; tbr; gaps were treated as fifth bases): a) Maximum parsimony for all data and b) Maximum likelihood for all data.

Bootstrapping (Felsenstein 1985) was performed for maximum parsimony with 1000 replicates and for maximum likelihood with 100 replicates.

The following analyses were conducted using MrBayes version 3.1.2 (Ronquist & Huelsenbeck 2003): Bayesian inference: a) all data (with one model for all three codon positions), b) all data (with codon specific models) and c) only codon position one and two (third codon position excluded; with one model for codon position one and two).

For Bayesian inference a Metropolis Chain Monte Carlo analysis with four chains and 1 000 000 generations was performed with the first 1000 trees ignored as burn-in.

3. RESULTS

3.1. Statistical tests

The sequences provided a total of 246 sites of which 105 were variable and 96 parsimony informative. Twenty-four (of 82) first base positions were variable as were 78 of the third base positions but only 3 of the second base positions. Insertion/deletion events (indels) were not observed in any of the groups. The amino acid alignment had no sites that were parsimony-informative within the Heterobranchia.

H3 analyses showed a high codon usage bias (Tab. 3). The bias was principally against the use of A and U in the third codon position. χ^2 tests were performed for all amino acids and revealed that the null hypothesis which is the expected equal usage of the codons can be rejected for all amino acids with a significance level of 0,001 excepting histidine ($p<0,05$). For aspartic acid the null hypothesis can not be rejected ($p=0,21$). The degree of bias ($\sum\chi^2/n$) showed a high value of 0,617.

Table 2. Information on used models.

Codon-Position	Model	Gamma distribution shape parameter	Proportion of invariable sites
1st Position	GTR+I	α=equal	Pinvar=0.5692
2nd Position	TVMef+I	α=equal	Pinvar=0.8647
3rd Position	TVM+G	α=0.8835	Pinvar=equal
1st and 2nd Position	GTR+I+G	α=0.9167	Pinvar=0.6909
1st, 2nd and 3rd Position	GTR+I+G	α=1.0265	Pinvar=0.5408

Table 3. Codon Usage Bias. N = number of times a particular codon is observed in a dataset (alignment). RSCU values = number of times a particular codon is observed, relative to the number of times that the codon would be observed in the absence of any codon usage bias. Amino acids (AA) are indicated by the three letter abbreviations.

AA	Codon	N	RSCU	AA	Codon	N	RSCU
Phe	UUU	6	(0.08)	Ser	UCU	45	(1.38)
Phe	UUC	142	(1.92)	Ser	UCC	34	(1.04)
Leu	UUA	3	(0.05)	Ser	UCA	13	(0.40)
Leu	UUG	43	(0.66)	Ser	UCG	8	(0.24)
Tyr	UAU	2	(0.04)	Cys	UGU	0	(0.00)
Tyr	UAC	96	(1.96)	Cys	UGC	0	(0.00)
Ter	UAA	0	(0.00)	Trp	UGG	0	(1.00)
Ter	UAG	0	(0.00)	Pro	CCU	83	(1.36)
Ter	UGA	0	(0.00)	Pro	CCC	107	(1.75)
Leu	CUU	48	(0.74)	Pro	CCA	42	(0.69)
Leu	CUC	81	(1.24)	Pro	CCG	13	(0.21)
Leu	CUA	2	(0.03)	Arg	CGU	233	(2.59)
Leu	CUG	214	(3.28)	Arg	CGC	127	(1.41)
His	CAU	31	(1.27)	Arg	CGA	18	(0.20)
His	CAC	18	(0.73)	Arg	CGG	9	(0.10)
Gln	CAA	41	(0.28)	Thr	ACU	53	(0.87)
Gln	CAG	252	(1.72)	Thr	ACC	146	(2.38)
Ile	AUU	21	(0.43)	Thr	ACA	45	(0.73)
Ile	AUC	126	(2.57)	Thr	ACG	1	(0.02)
Ile	AUA	0	(0.00)	Ser	AGU	8	(0.24)
Asn	AAU	0	(0.00)	Ser	AGC	88	(2.69)
Asn	AAC	0	(0.00)	Arg	AGA	74	(0.82)
Lys	AAA	135	(0.61)	Arg	AGG	78	(0.87)
Lys	AAG	306	(1.39)	Ala	GCU	201	(1.49)
Val	GUU	9	(0.18)	Ala	GCC	279	(2.07)
Val	GUC	89	(1.82)	Ala	GCA	47	(0.35)
Val	GUA	4	(0.08)	Ala	GCG	12	(0.09)
Val	GUG	94	(1.92)	Gly	GGU	32	(0.87)
Asp	GAU	38	(0.78)	Gly	GGC	38	(1.03)
Asp	GAC	60	(1.22)	Gly	GGA	72	(1.96)
Glu	GAA	69	(0.70)	Gly	GGG	5	(0.14)
Glu	GAG	128	(1.30)	Met	AUG	49	(1.00)

The consistency index in maximum parsimony analyses was low (0,210) as well as the retention index (0.444). Using the method developed by Xia et al. (2003) a substitution saturation was observed in the third codon position (I_{ss} 0,543 > $I_{ss\cdot c}$ 0,298). To support this observation the entropy for each position in the alignment was calculated using BioEdit Version 7.0.5.2. Codon position one showed an average entropy value of 0,09 whereas the value for the second codon position was 0,009 and 0,69 for the third codon position. If the nucleotides occur more or less equally at a certain position within the alignment the entropy is highest with the value of 1,36.

3.2. Phylogenetic analyses

The maximum parsimony 50 % majority-rule consensus tree (Fig. 1) showed all genera (*Aplysia, Elysia, Onchidella, Siphonaria, Orbitestella, Turbonilla* and *Rissoella*) recovered as monophyletic. However, some of the bootstrap supports were low and there was no bootstrap support for a monophyletic *Rissoella*. Beyond the genera level, only Architectonicoidea were detected as monophyletic. All other nodes lacked support.

The genera *Orbitestella*, *Turbonilla*, *Onchidella* and *Aplysia* and again, the Architectonoicoidea were found to be monophyletic in the maximum likelihood analyses. The

Fig. 1. 50 % majority-rule consensus tree of maximum parsimony of 14 most parsimonious trees based on histone H3 data set (nucleotides), number of parsimony informative characters = 96, consistency index (CI) = 0,210.

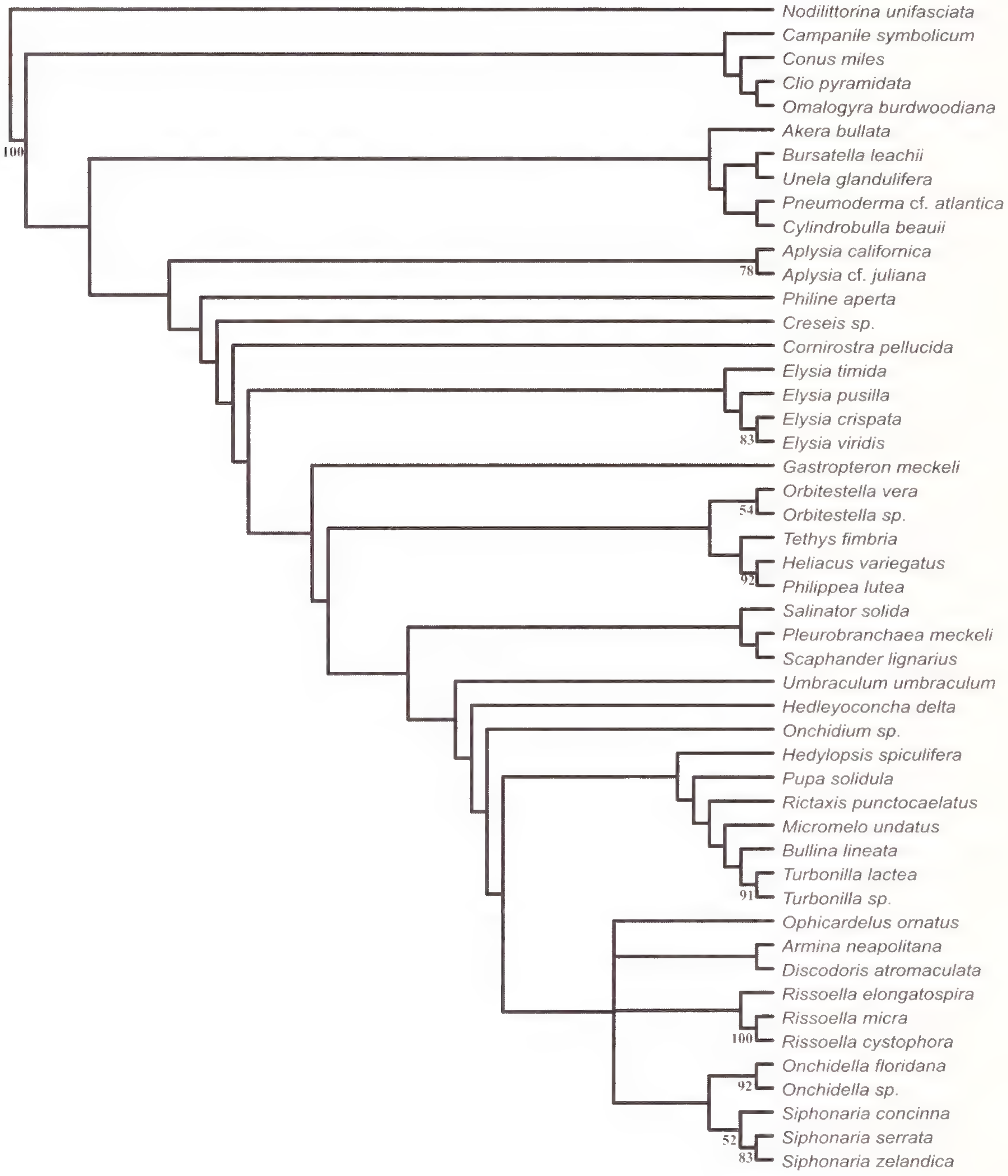

Nodilittorina unifasciata
Campanile symbolicum
Conus miles
Clio pyramidata
Omalogyra burdwoodiana
Akera bullata
Bursatella leachii
Unela glandulifera
Pneumoderma cf. *atlantica*
Cylindrobulla beauii
Aplysia californica
Aplysia cf. *juliana*
Philine aperta
Creseis sp.
Cornirostra pellucida
Elysia timida
Elysia pusilla
Elysia crispata
Elysia viridis
Gastropteron meckeli
Orbitestella vera
Orbitestella sp.
Tethys fimbria
Heliacus variegatus
Philippea lutea
Salinator solida
Pleurobranchaea meckeli
Scaphander lignarius
Umbraculum umbraculum
Hedleyoconcha delta
Onchidium sp.
Hedylopsis spiculifera
Pupa solidula
Rictaxis punctocaelatus
Micromelo undatus
Bullina lineata
Turbonilla lactea
Turbonilla sp.
Ophicardelus ornatus
Armina neapolitana
Discodoris atromaculata
Rissoella elongatospira
Rissoella micra
Rissoella cystophora
Onchidella floridana
Onchidella sp.
Siphonaria concinna
Siphonaria serrata
Siphonaria zelandica
100
78
83
54
92
91
100
92
52
83

Fig. 2. 50 % majority rule consensus Bayesian inference cladogram for the histone H3 dataset (based on nucleotides); Bayesian posterior probabilities provided at the branches.

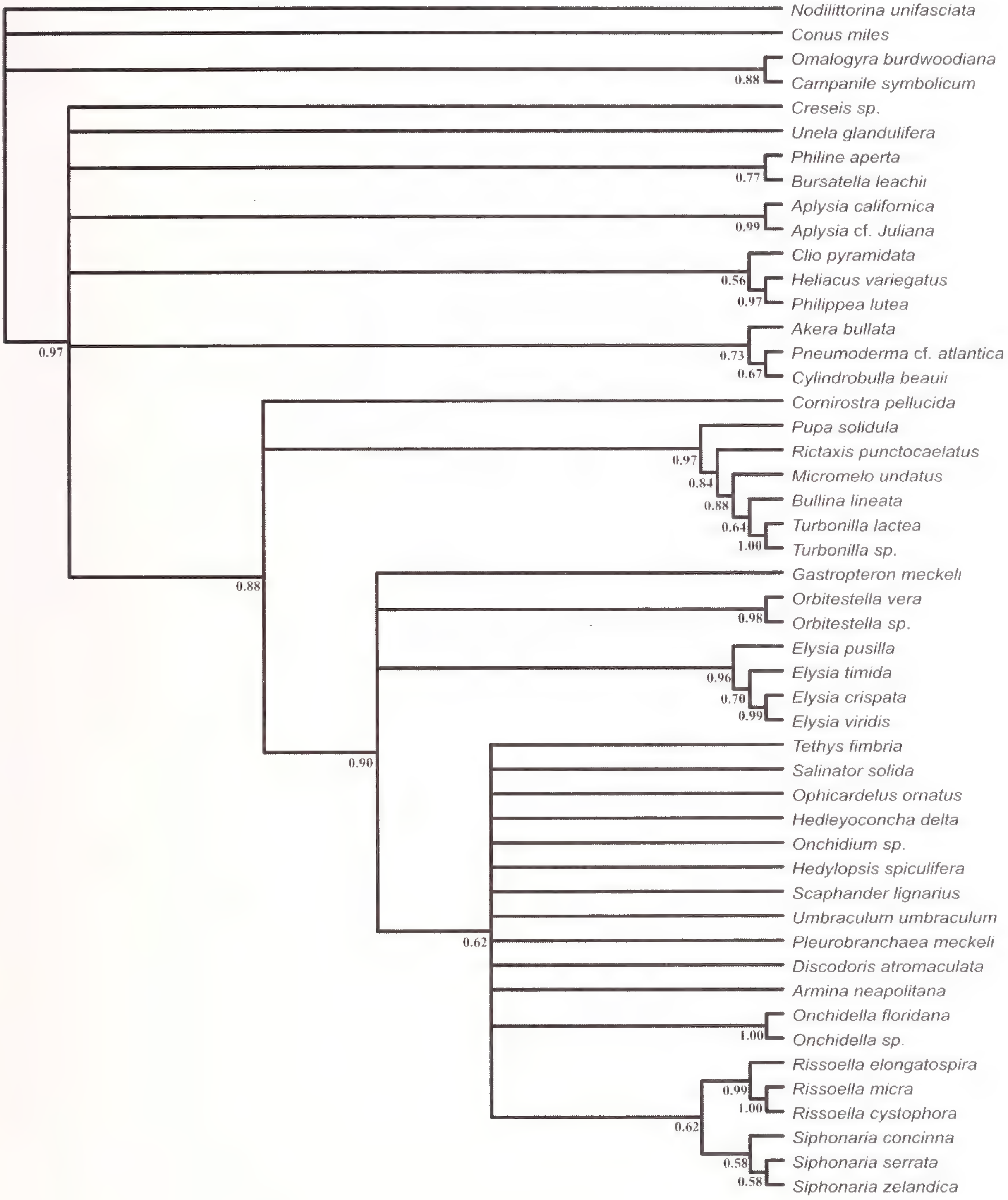
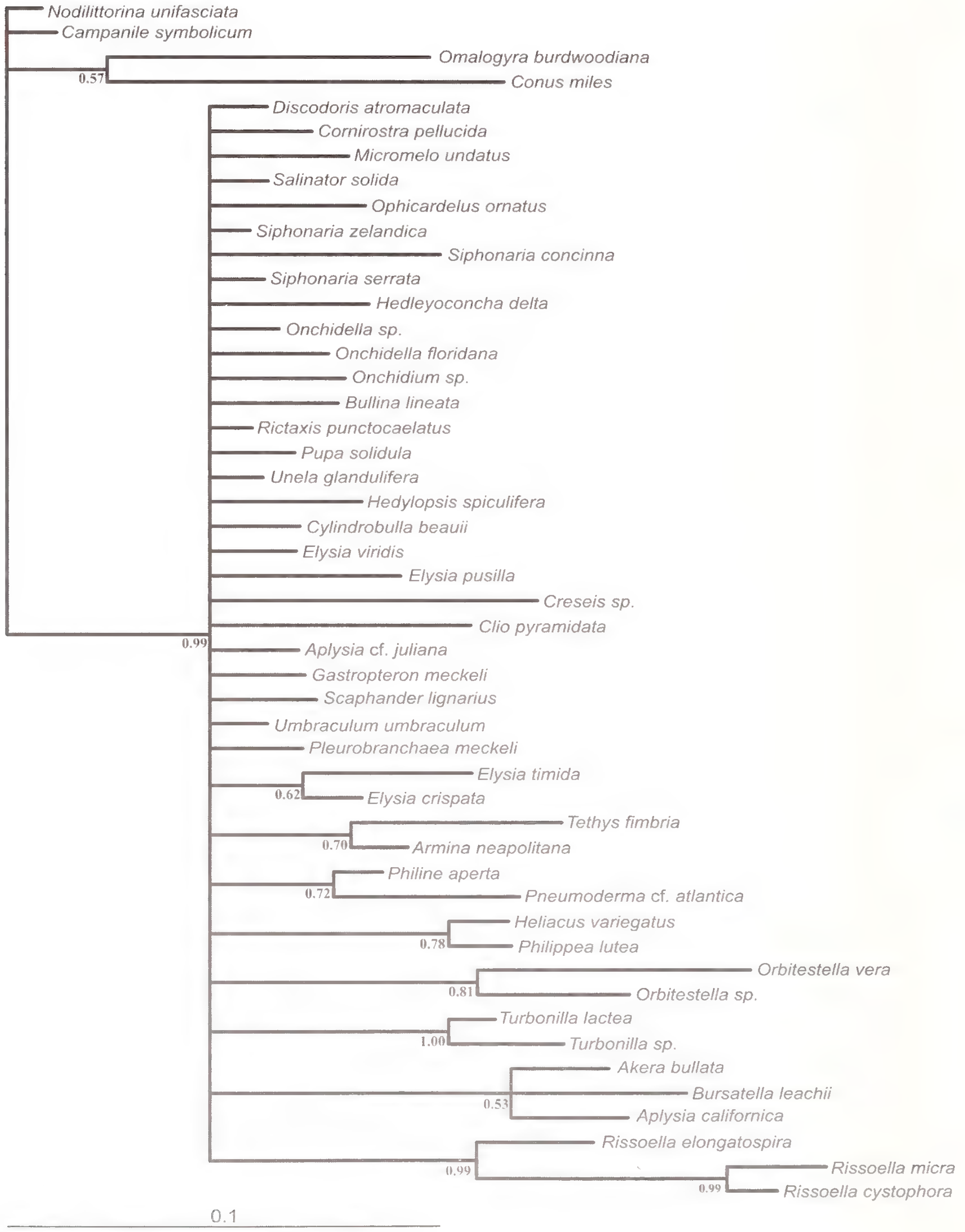

Nodilittorina unifasciata
Conus miles
Omalogyra burdwoodiana
0.88
Campanile symbolicum
Creseis sp.
Unela glandulifera
Philine aperta
0.77
Bursatella leachii
Aplysia californica
0.99
Aplysia cf. Juliana
Clio pyramidata
0.56
Heliacus variegatus
0.97
Philippea lutea
Akera bullata
0.97
0.73
Pneumoderma cf. atlantica
0.67
Cylindrobulla beauii
Cornirostra pellucida
Pupa solidula
0.97
Rictaxis punctocaelatus
0.84
Micromelo undatus
0.88
Bullina lineata
0.64
Turbonilla lactea
1.00
Turbonilla sp.
Gastropteron meckeli
0.88
Orbitestella vera
0.98
Orbitestella sp.
Elysia pusilla
0.96
Elysia timida
0.70
Elysia crispata
0.99
Elysia viridis
Tethys fimbria
0.90
Salinator solida
Ophicardelus ornatus
Hedleyoconcha delta
Onchidium sp.
Hedylopsis spiculifera
Scaphander lignarius
Umbraculum umbraculum
0.62
Pleurobranchaea meckeli
Discodoris atromaculata
Armina neapolitana
Onchidella floridana
1.00
Onchidella sp.
Rissoella elongatospira
0.99
Rissoella micra
1.00
Rissoella cystophora
0.62
Siphonaria concinna
0.58
Siphonaria serrata
0.58
Siphonaria zelandica

Fig. 3. 50 % majority rule consensus Bayesian inference phylogram for the histone H3 dataset (based on nucleotides, 3rd codon position excluded); Bayesian posterior probabilities provided at the branches.


Nodilittorina unifasciata
Campanile symbolicum
Omalogyra burdwoodiana
0.57
Conus miles
Discodoris atromaculata
Cornirostra pellucida
Micromelo undatus
Salinator solida
Ophicardelus ornatus
Siphonaria zelandica
Siphonaria concinna
Siphonaria serrata
Hedleyoconcha delta
Onchidella sp.
Onchidella floridana
Onchidium sp.
Bullina lineata
Rictaxis punctocaelatus
Pupa solidula
Unela glandulifera
Hedylopsis spiculifera
Cylindrobulla beauii
Elysia viridis
Elysia pusilla
Creseis sp.
Clio pyramidata
0.99
Aplysia cf. juliana
Gastropteron meckeli
Scaphander lignarius
Umbraculum umbraculum
Pleurobranchaea meckeli
Elysia timida
0.62
Elysia crispata
Tethys fimbria
0.70
Armina neapolitana
Philine aperta
0.72
Pneumoderma cf. atlantica
Heliacus variegatus
0.78
Philippea lutea
Orbitestella vera
0.81
Orbitestella sp.
Turbonilla lactea
1.00
Turbonilla sp.
Akera bullata
Bursatella leachii
0.53
Aplysia californica
Rissoella elongatospira
0.99
Rissoella micra
0.99
Rissoella cystophora
0.1

basis of the 50 % majority-rule bootstrap tree (tree not shown) resembled a comb. There was no resolution of the deep nodes.

The 50 % majority-rule consensus Bayesian inference cladogram (with one model for all three codon positions) (Fig. 2) also recovered all genera as monophyletic. Only the Bayesian posterior probability for *Siphonaria* was low (0.58) because only values above 0.95 are statistically significant. Beside the genera level Architectonicoidea were monophyletic and the Caenogastropoda formed a clade together with *Omalogyra*. All other nodes had no statistically significant support.

The 50 % majority-rule consensus Bayesian inference cladogram (with codon specific models) (tree not shown) was quite similar to Figure. 2. All genera except *Rissoella* and Architectonicoidea were found to be monophyletic. The remaining nodes were supported by Bayesian posterior probabilities below 0.95.

The 50 % majority rule consensus Bayesian inference phylogram (with 3^rd^ codon position excluded and with one model for codon position one and two) (Fig. 3) recovered only the genera *Rissoella* and *Turbonilla* as monophyletic while the Caenogastropoda together with *Omalogyra* were grouped separately from the rest of the taxa. All other nodes had no statistically significant support.

4. DISCUSSION

Molecular investigations of deep-level relationships within the Gastropoda have been made difficult due to a lack of slowly evolving genes. Hence, a number of different markers have been utilized to solve this problem. Analyses of nuclear genes like the 28S ribosomal RNA and/or the 18S ribosomal RNA have provided a number of important insights into gastropod relationships at several levels (Tillier et al. 1994, 1996; Dayrat et al. 2001; Vonnemann et al. 2005). The same applies to mitochondrial genes like the 16s ribosomal RNA (Thollesson et al. 1999) or the cytochrome oxidase subunit I (Remigio & Hebert 2003). Colgan et al. (2000, 2003) used the histone H3 protein in combination with other genes to clarify gastropod molecular evolution. However, many aspects of gastropod phylogeny remain unclear such as the molecular confirmation of the Heterobranchia concept based on morphological studies from Haszprunar (1985, 1988). At the moment there is no comprehensive molecular study of heterobranch phylogeny especially one including the “basal” taxa (e. g. Pyramidelloidea, Architectonicoidea, Valvatoidea, Omalogyroidea and Rissoelloidea).

In this study we wanted to present a primary molecular insight into heterobranch phylogeny while simultaneously testing the utility of the gene coding for the highly conserved protein histone H3 for resolving the deeper nodes within this taxon.

Unfortunately, the present study did not provide a robust phylogenetic hypothesis for the relationships among different lineages of Heterobranchia based on H3-Genesequences. Neither the monophyly of the Euthyneura nor a step-by-step evolution by the “basal” groups was supported. A conclusion about the monophyly of Opisthobranchia and Pulmonata could not be extracted from our data because we did not have any resolution at this point.

The first to investigate the value of histone H3 were Colgan et al. (1998). They wanted to combine small nuclear ribonucleic acid U2 data and histone H3 to investigate arthropod molecular evolution. However, partitioned data for H3 and U2 were incongruent according to Incongruence Length Difference tests. Using H3 data only, anomalous nodes appeared in their phylogenies while some possessed decay indices of 1. Therefore, their data were not sufficient to clarify relationships within major arthropod groups.

Brown et al. (1999) investigated the DNA sequence data of 34 Polychaeta species for partial histone H3, U2 snRNA and two segments of 28S rDNA (D1 and D9-10 expansion regions). When using H3 only, Brown et al. (1999) found a lack of concordance with morphological results and argued that the inclusion of all H3 data is inappropriate for the phylogenetic levels under investigations.

Colgan et al. (2000) and later Colgan et al. (2003) used partial histone H3 (327bp) for the investigation of gastropod phylogeny. In Colgan et al. (2000), where the authors used 36 sequences of histone H3 only, using the chiton *Ischnochiton australis* as an outgroup, no clades were retained in the bootstrap analyses. H3 with the third codon position excluded, retained only the higher Vetigastropoda (bootstrap support = 68 %).

In Colgan et al. (2003) in which H3 alone was used to recover phylogenetic relationships within Gastropoda, only the clade of the Patellogastropoda with a support of 52 % was recovered. When the third codon position was excluded, none of the expected groups were recovered.

Okuso et al. (2003) were the first to apply DNA sequence data to reconstruct the phylogeny of the molluscan class Polyplacophora. Their use of 59 sequences of histone H3 resolved deeper nodes than the mitochondrial genes did while the strict consensus tree nested the two Gastropoda *Viviparus georgianus* and *Siphonaria pectinata* within Polyplacophora.

A combined approach to the phylogeny of Cephalopoda (Mollusca) using 18S rRNA, 28S rRNA, histone H3 and COI underscored the aim of the study presented by LINDGREN et al. (2004). The strict consensus tree for the overall optimal parameter set for 66 sequences of histone H3 alone did not show monophyly for any classes investigated.

KJER et al. (2006) investigated the molecular phylogeny of Hexapoda (supermatrix approach with 137 taxa; 375bp). They only recovered one ordinal level node when using only H3.

According to our phylogenetic results and the results in the papers listed above histone H3 alone provides no new marker for studying deep molecular evolution of the Heterobranchia due to the high grade of conservation and the low phylogenetic signal for deeper nodes.

There were several indices defined by the results of our statistical tests supporting this assumption. We observed a high codon usage bias (see tab. 2) in our alignment which was also indicated by an increasing frequency of C- and G-ending codons and fewer A- and U-ending codons (SHIELDS et al. 1988). High C+G content at silent sites reflects the effect of selection (SHIELDS et al. 1988) while selective constraints against certain codons might reduce the amount of phylogenetic noise caused by synonymous substitution at either first or third codon positions (BROWN et al. 1999). However, our data suggest that a bias in codon usage will not necessarily be indicative of the phylogenetic utility of a sequence. Despite a high codon usage bias our computed phylogenetic trees showed a poor resolution of the deeper nodes. An explanation for this could be that the pressure to obtain the favoured codon had partially obscured the phylogenetic signal. COLGAN et al. (1998, 2000) made similar observations and concluded that apparent, high codon-usage bias as found for the H3 data does not necessarily result in high phylogenetic consistency for DNA sequences. In the studies presented by BROWN et al. (1999) a lack of agreement of the H3 analyses with morphology occurs despite very high codon usage bias. They concluded that whilst selective constraints may have reduced the absolute rate of synonymous substitutions, the pressure in favor of (homoplastic) restitution of the favoured codon has at least a partially obscured phylogenetic signal. Hence, codon usage bias does not necessarily mean that a gene sequence will be phylogenetically useful.

The degree of bias ($\sum\chi^2/n$) showed a high value of 0,617. It was similar to the values observed in gastropods (0.60) (COLGAN et al. 2000) and polychaetes (0.665) (Brown et al. 1999) and higher than the values of *Drosophila melanogaster* (FITCH & STRAUSBAUGH 1993) and arthropods (0.37) (COLGAN et al. 1998).

Another indication suggesting the problems of H3 as a marker for studying deep molecular evolution was the high grade of conservation indicated by the lack of parsimony-informative sites in the amino acid alignment.

Additional important evidence was the observed substitution saturation at the third codon position. A saturation is caused by multiple-hits which render homoplasious changes. Homoplasy on the basis of saturation in substitution is one of the major problems in molecular phylogenetics (TILLIER et al. 1996). This problem generally becomes more relevant at progressively higher taxonomic levels (BOORE & BROWN 1998). If numerous substitutions occur at the same position, a hiding or completely erasing of the ancient phylogenetic signal could be the result (LOPEZ et al. 1999). In order to avoid a decrease of the phylogenetic information contained in the sequences, we excluded the third codon position in further analyses. However, this was the position with the most variable sites (78 of 82 positions) in our data set. With the exclusion there was no phylogenetic information left for a resolution of the deeper nodes. Trees which resemble combs at the base resulted (see fig. 3). The entropy was calculated for each position in the alignment to further assess the influence of the 3 codon positions. A high entropy value implies that the nucleotides occur almost equally at this position within the alignment. An almost equal distribution of the nucleotides at one position indicates a less selective constraint allowing a higher frequency of substitutions. The average values for each of the three codon positions indicate a less selective constraint for the third codon position hence supporting the previous result of this codon position being saturated.

It is questionable if given a larger data set, the noise will eventually succumb to the signal. There are few examples where the expansion of an ambiguous data set has resulted in a convincing phylogeny (BOORE & BROWN 1998).

Surprisingly, there was a good resolution on genera level. Analyses conducted with maximum parsimony and Bayesian inference (with all data) recovered all (or nearly all) genera mostly with statistically significant supported nodes. However, our findings should be consider preliminary and further studies including more genera are necessary to test the possible utility of histone H3 for the resolution of recent splits. In other studies (COLGAN et al. 1998; OKUSO et al. 2003; LINDGREN et al. 2004) some (but not all) genera were found to be monophyletic but due to the question the authors intended to answer, their studies in regards to taxon sampling lacked genera represented by more than one species.

In conclusion, still slowly evolving genes for the resolution of the deeper nodes in gastropod phylogeny are missing. To test the Heterobranchia concept as outlined by HASZPRUNAR (1988) other markers have to be found with sufficient variability but no substitution saturation.

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Biogeographic considerations of the Opisthobranchia (Mollusca: Gastropoda) fauna from the Brazilian littoral and nearby areas*

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Abstract. The aim of this paper is to examine the biogeographical distribution of the littoral and sub-littoral opisthobranch gastropods from Brazil and nearby areas. On the basis of published literature and personal data, a zoogeographic study was undertaken and the Brazilian region was compared with the Caribbean and Argentinean regions. The Brazilian littoral has been divided into six zones, based in the oceanographic features established by CASTRO & MIRANDA (1998). 466 species belonging to the orders Cephalaspidea, Anaspidea, Sacoglossa, Notaspidea and Nudibranchia from the Caribbean to the Argentinean region were considered in this study. The number of opisthobranch species is highest in Caribbean areas. Along the Brazilian littoral, South Brazilian Bight is the region with highest richness, while Orinoco-Amapá and Amazon shelf are the areas with lower species numbers. The similarity analysis shows that some possible geographic barriers act to the distribution of the opisthobranchs. For each locality considered in the study, the percentage of species that extends northward is higher than southward.

Keywords. Brazil, Caribbean region, Argentinean region, biogeography, species list.

1. INTRODUCTION

Faunistic inventories give fundamental information for many basic and applied scientific disciplines, such as ecology and biogeography (STORK & SAMWAYS 1995). An essential tool to establish inventories is taxonomy, which supplies a reference system for the biodiversity (BISBY 1995). The level of faunistic and taxonomical knowledge from different regions varies considerably, which raises a problem for the accomplishment of biogeographic studies. Nevertheless, the elaboration of this type of studies offers insights into possible models of distribution of a taxonomic group throughout a more or less extensive area.

Opisthobranch gastropods are well represented in most marine habitats from equatorial to polar regions. Ernst and Eveline Marcus studied this group for more than thirty years in West Atlantic temperate and warmer waters. Recently, other authors have provided new contributions to the knowledge of the Brazilian opisthobranchs (TRONCOSO et al. 1998; GARCÍA et al. 2002; GARCÍA & TRONCOSO 2003, 2004; PADULA & ABSALÃO 2005; POLA et al. 2005; DOMÍNGUEZ et al. 2006 a, b; VALDÉS et al. 2006). The actual level of knowledge of the opisthobranchs from Brazilian and Caribbean regions (i.e. MARCUS 1977; MARCUS & MARCUS 1967a; THOMPSON 1977, 1980; ESPINOSA & ORTEA 2001; ROSENBERG 2005; VALDÉS et al. 2006) permits some biogeographical considerations; however, future studies along some areas of Brazilian coast are necessary to obtain a more complete knowledge of this fauna. The work of Marcus and Marcus was focused around São Paulo and Rio de Janeiro areas. The necessity of more faunistic studies in Brazil is obvious when comparing the number of species cited along Brazilian coasts (280 species, after MARCUS 1977) with, for example, the Iberian Peninsula (523 species, after CERVERA et al. 2004).

Here, we present a study on the diversity of the Opisthobranchs along the Brazilian coasts, using as biogeographic areas the six zones defined by CASTRO & MIRANDA (1998). These Brazilian zones are also compared with Caribbean and Argentinean regions (i.e. MUNIAIN 1997; SCHRÖDL 1999; ROSENBERG 2005).

2. MATERIAL AND METHODS

2.1. Biogeographical areas

This research was conducted by comparing littoral and sub-littoral Opisthobranch fauna from the Brazilian shores with those from the Caribbean and Argentinean biogeographic regions. Species checklists were compiled by combining data from bibliographical sources and personal observations (included in the references). The total number of species considered for this study is 466, belonging to the orders Cephalaspidea, Anaspidea, Sacoglossa, Notaspidea and Nudibranchia (Table 1).

In this paper, we adopted the six oceanographic zones defined in CASTRO & MIRANDA (1998) for Brazil (Fig. 1). The geographical limits and features of these areas are shown in Table 2.

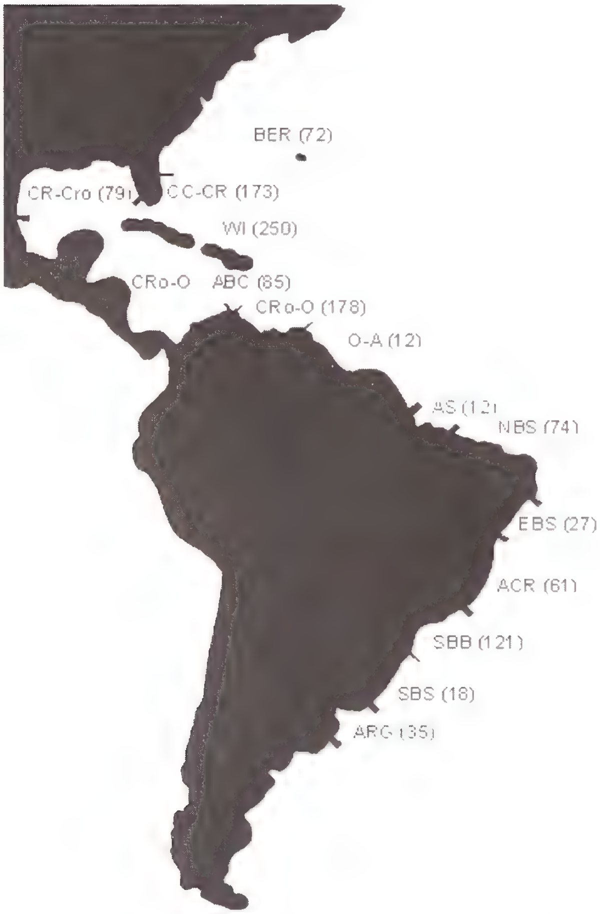


Fig. 1. Limits of the areas considered along Brazilian coasts, based on CASTRO & MIRANDA (1998) and nearby zones based on BRIGGS (1974). The number of species considered for each region is indicated.

Within the Caribbean region we have considered the provinces defined in BRIGGS (1974) (Fig. 1):

CC-CR, extends from Cape Canaveral to Cabo Romano

CR-CRo, extends from Cape Romano to Cape Rojo

CRo-O, extends from Cape Rojo to the mouth of the Orinoco River

O-A, extends from Orinoco River to Amapá

ABC, Includes Aruba, Bonaire and Curaçao

WI West Indies (WI)

Bermudas Is (BER).

In addition, we consider the Argentinean region (ARG) between the borders of Brazil to Uruguay up to 43-44°S (Chubut).

2.2. Community analysis and measurement of biodiversity

In order to examine diversity within the opisthobranch communities, data by region were subjected to a multivariate analysis using the Bray Curtis similarity measure and non-metric Multidimensional Scaling Ordination (MDS).

The Bray-Curtis index (BRAY & CURTIS 1957) was chosen because it does not consider double absences in its calculations. The results were then graphically described using dendrograms with the UPGMA (unweighted pair-group methods using arithmetic averages) aggregation algorithm (SNEATH & SOKAL 1973). The ordination analyses were carried out by means of an MDS (non metric multidimensional scaling program) based on the similarity matrix between stations.

For two different station groups a requirement is to identify which species account for the observed assemblage difference (CLARKE & GORLEY, 2001). The SIMPER routine was used to identify taxa that greatly contributed to differentiate station groups. The software used was P.R.I.M.E.R. (Plymouth Routines in Multivariate Ecological Research) version 5.2.8. for Windows.

3. RESULTS

466 species of opisthobranchs were found to occur in the Western Atlantic Ocean from Cape Canaveral to the Argentinean province (the Atlantic Magellanic region is not included). Table 3 shows the number of species by order or suborder for each zoogeographic area. The number of

opisthobranch species for each area varies remarkably. WI (West Indies) has the highest number of species (250 species), although, in general, the number is also high in the Caribbean areas Cro-O and CC-CR. Along the Brazilian zones, the number of species is lower and there is also a notable difference between the different zones. SBB is the zone with the highest number of species while AS is the zone with the lowest number (122 and 12 species, respectively). The number of species from the Argentinean region (ARG) is moderately low.

3.1. Faunal affinities

The cluster analysis using the six Brazilian zones shows a first division in which AS separate from the remaining zones (Fig. 2A). A second division separates SBS, and finally, the rest of the areas splits into two groups; a group including the north-eastern Brazilian zones EBS and NBS, and the other including ACR and SBB. A two-dimensional representation of the analysis MDS shows this same grouping pattern (Fig. 2B).

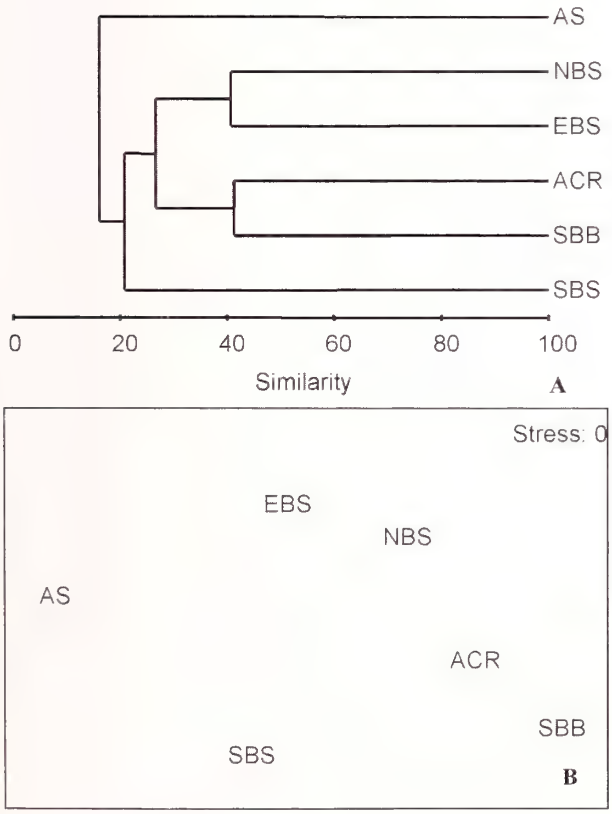


Fig. 2. Cluster classification (A) and MDS ordination (B) of the biogeographic areas based on the presence-absence of species in the areas from Brazil.

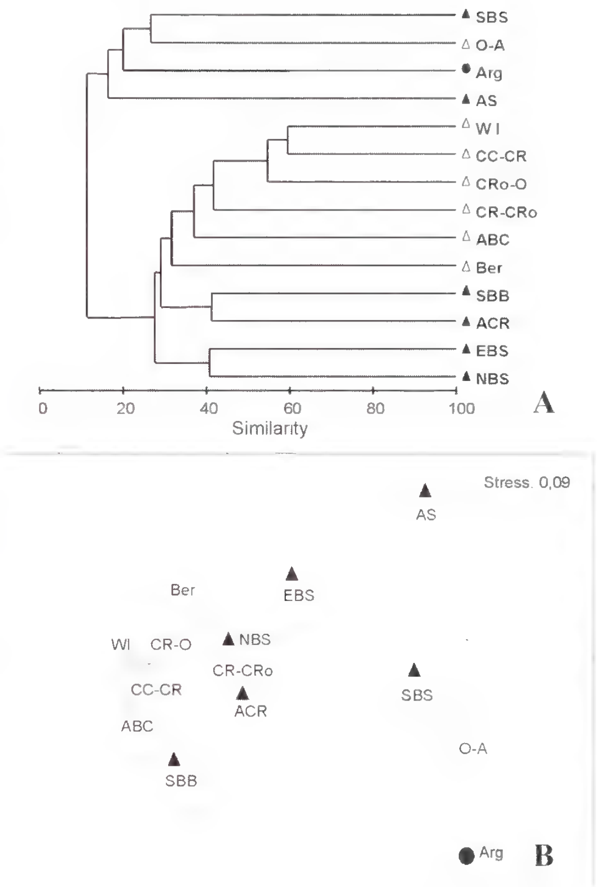


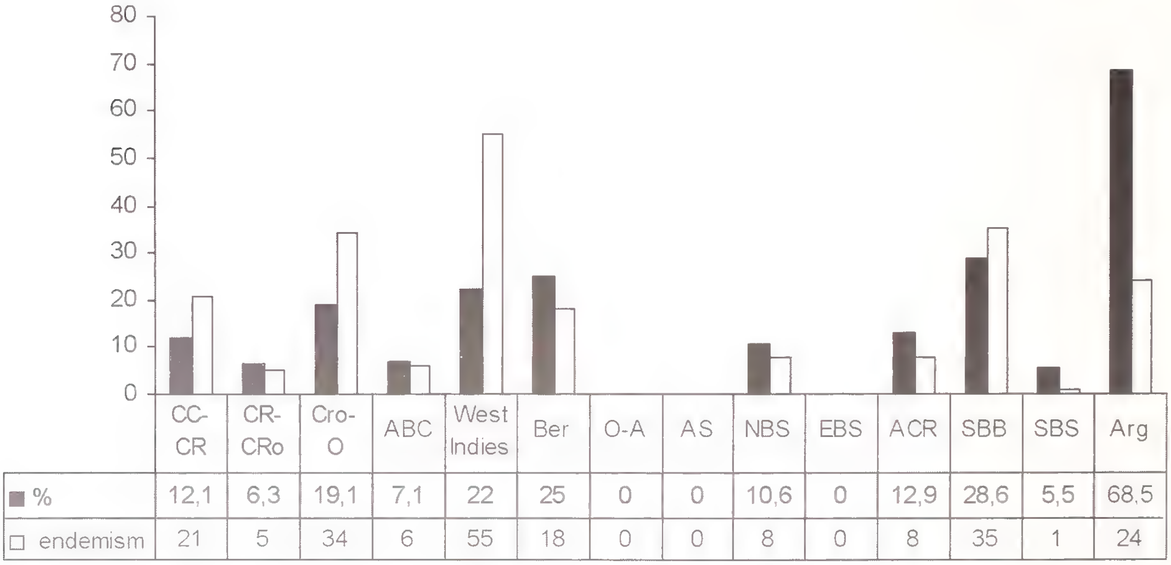
Fig. 2. Cluster classification (A) and MDS ordination (B) of the biogeographic areas based on the presence-absence of species in all areas included in this study. Black triangles, Brazilian regions; white triangles. Caribbean provinces; black circle, Argentinean region.

Including all geographical areas from Cape Canaveral and Bermudas to Chubut (Argentinean region), the cluster analysis and MDS show a first division in which Orinoco-Amapá (O-A), the Brazilian areas SBS and AS and the Argentinean region (ARG) separate from the remaining regions (Fig. 3). Those separate in two groups. One includes the north-eastern Brazilian zones EBS and NBS, while the other includes the remaining zones. The latter divides itself into two subgroups, one including the Brazilian regions SBB and ACR, and the other subgroup including all Caribbean provinces.

The SIMPER analysis identified four distinct groups. In group 1 (SBS, O-A, ARG, AS), the following taxa contribute to the similarity (up to 85%): Cephalaspidea (*Acteocina bidentata, Volvulella persimilis, Acteocina candei, Acteon pelecais*) and Notaspidea (*Pleurobranchaea inconspicua*). Group 2 (WI, CC-CR, CRo-O, CR-CRo, ABC, Ber) is mainly characterised by species of the orders Cephalaspidea (*Volvulella, Bulla, Haminoea, Hydatina, Micromelo*), Notaspidea (*Umbraculum, Pleurobranchus*), Anaspidea (*Stylocheilus, Bursatella, Aplysia, Bosellia*), Sacoglossa (*Cylindrobulla, Oxynoe, Tridachia, Elysia)* Dendronotacea (*Scyllaea*) and Nudibranchia (*Spurilla, Chromodoris*). Group 3 (SBB, ACR) is characterised by the presence of species of the order Nudibranchia, mainly Doridina (*Dendrodoris krebsii, Cadlina rumia, Tyrinna evelinae, Diaulula greeleyi, Discodoris evelinae, Chromodoris clenchi*), Armінina (*Armina*) and Aeolidina (*Spurilla neapolitana, Phidiana lynceus, Flabellina engeli, Glaucus atlanticus*). Group 4 (EBS, NBS) is determined (up to a cumulative 90%) by the presence of the orders Nudibranchia (*Doto divae, Diaulula greeleyi*), Notaspidea (*Pleurobranchaea inconspicua, Umbraculum umbraculum, Berthellina quadridens*), Anaspidea (*Phyllaplysia engeli, Stylocheilus striatus, Aplysia dactylomela, Aplysia parvula, Bursatella leachii*), Saccoglossa (*Cylindrobulla beauii, Oxynoe antillarum, Elysia tuca*), and Cephalaspidea (*Philine sagra, Hydatina vesicaria, Micromelo undatus, Haminoea elegans, Chelidonura petra*)

In terms of dissimilarity, the species *Spurilla neapolitana, Scyllaea pelagica, Pleurobranchus areolatus, Tridachia crispata, Aplysia dactylomela, Aplysia fasciata, Oxynoe antillarum* contribute greatly to differentiate groups 1 and 2. Group 1 differed from group 3 due to *Phidiana lynceus, Spurilla neapolitana, Flabellina engeli, Facelina coenda, Anteaeolidiella indica, Berghia benteva, Taringa telopia, Tyrinna evelinae, Siraius ilo, Jorunna spazzola, Okenia zoobotryon, Hallaxa apefae, Doris verrucosa, Discodoris evelinae, Chromodoris neona, Dendrodoris krebsii, Diaulula greeleyi, Cadlina rumia, Chromodoris clenchi, Berthella agassizii, Berthella stellata, Aplysia dactylomela, Aplysia fasciata, Oxynoe antillarum, Ascobulla ulla, Navanax aenigmaticus.* Group 1 differed from group 4 due to *Doto divae, Diaulula greeleyi, Phyllaplysia engeli, Stylocheilus striatus, Berthellina quadridens, Aplysia dactylomela, Aplysia parvula, Oxynoe antillarum, Elysia tuca, Micromelo undatus, Chelidonura petra, Atys riiseanus*. Differences between group 2 and group 4 were mainly due to *Tridachia crispata, Aplysia fasciata, Chelidonura petra.* The group 2 differed from group 3 due to *Facelina coenda, Berghia benteva, Scyllaea pelagica, Siraius ilo, Hallaxa apefae, Chromodoris neona, Tridachia crispata, Philine mera, Cylindrobulla beauii, Acteon pelecais.* And finally the species *Phidiana lynceus, Flabellina engeli, Glaucus atlanticus, Facelina coenda, Armina muelleri, Anteaeolidiella indica, Berghia benteva, Doto divae, Taringa telopia, Tyrinna evelinae, Siraius ilo, Okenia zoobotryon, Hallaxa apefae, Chromodoris neona, Dendrodoris krebsii, Cadlina rumia* explained most of the dissimilarity between groups 3 and 4.

Figure 4 shows the number and percentage of endemic species for each biogeographic area. Those species considered as endemic have been cited only at one zoogeographic region from the area of study. Geographic distribution along other biogeographic regions was not considered for this study. The level of endemism varies notably along the different zoogeographic areas. The highest value was found in the Argentinean region (68.6%). This high value is due to a southward distribution to the Magellan region of the fauna from this area. The Brazilian zones



	CC-CR	CR-CRo	Cro-O	ABC	West Indies	Ber	O-A	AS	NBS	EBS	ACR	SBB	SBS	Arg
■ %	12,1	6,3	19,1	7,1	22	25	0	0	10,6	0	12,9	28,6	5,5	68,5
□ endemism	21	5	34	6	55	18	0	0	8	0	8	35	1	24

Fig. 4. Number and percentage of endemic species for each faunistic area.

have percentages between 0 % in Amazon Shelf (AS) and East Brazilian Shelf (EBS), and 28.7 % in South Brazilian Bight (SBB). Among the Caribbean provinces, the percentage of endemism varies between 7.1 %, at Aruba, Bonaire and Curaçao (ABC), and 22 % in the West Indian region.

Table 4 shows the percentage of species from each region present in other localities. The percentage is increasing, when extended northward, and decreasing, when extended southward.

4. DISCUSSION

An aspect to be considered in this study is that the data on species distribution and the level of knowledge of the communities vary across the geographical regions. Thus, the results presented here must be considered as tentative.

The number of opisthobranch species between biogeographic areas varies remarkably being higher in the Caribbean: West Indies (WI: 250 species), Cape Rojo-Orinoco (CRo-O: 178) and Cape Canaveral-Cape Romano (CC-CR: 173). The south Brazilian Bight (SBB) is the zone in Brazil with the highest richness (122 species), followed by the north Brazilian Shelf (NBS: 75) and the Abrolhos-Campos Region (ACR: 62). The areas with the lowest species richness are Oricono-Amapá (O-A) and Amazon Shelf (AS), both with 12 species, followed by South Brazilian Shelf (SBS) with 18 species. This could be related to oceanographic conditions, such as the effect of the Amazon River in the AS zone, and with a difference in sampling effort; the south Brazilian Bight is the zone where Ernst and Eveline Marcus did many of their collections.

The first division observed in the similarity analysis includes four geographical regions with features that seem to act as barriers to the distribution of opisthobranchs. The coasts from Orinoco-Amapá and Amazon Shelf are influenced by the Amazon and Orinoco rivers whose plumes spread north-westward for more than 1,000 km into the North Atlantic (CASTRO & MIRANDA 1998). These areas are characterised by soft bottom, turbid waters and freshwater runoff and they have been recognised as barriers to the dispersal of corals (COX & MOORE 2000), rocky shore gastropods (VERMEIJ 1978) and shallow water reef fishes (GILBERT 1972). The scarce opisthobranch fauna from Orinoco-Amapá and Amazon Shelf and the composition of species present in these areas are likely related to environmental characteristics of the region. Species present in these areas are generally cephalaspideans and arminacean, which frequently live in sand or mud. A similar situation is found on the South Brazilian Shelf, where the low species numbers may be related to the effect of the Patos Lagoon River plume with an annual mean discharge of about 2000 m^3s^{-1} (MARQUES et al. 2006). This area is influenced during the winter by Subantarctic water.

The coastal area of the Argentinean biogeographic province is a transition zone characterised by processes of mixing and instability of the water masses. This province includes geographical features like the Rio de la Plata. The estuaries influence the primary and secondary production in the area and consequently, the distribution of species. Moreover, there is an interaction off the coast between the Malvinas current flowing on the slope from the south with cold Subantarctic waters rich in nutrients and the Brazilian current, with temperatures higher than 20° C and salinity over 36.0 ppt. This determines the presence of eurythermal and euryhaline species (BOSCHI 2000). The fauna of opisthobranchs is formed mainly by nudibranchs, which have their northern distribution limit at the border between the Argentinean region and the South Brazilian Shelf, extending southwards to Subantarctic regions.

Cluster analyses show two Brazilian groups, composed of NBS-EBS and ACR-SBB. In general, these groups coincide geographically with those indicated by FLOETER et al. (2001) to the reef-fish fauna of the Brazilian coast. These authors considered several regions like the South and South-eastern coastal reefs, from the Guarapari islands to Santa Catarina (areas included in our analysis as the group ACR-SBB), and the North-eastern coast, extending from the Manuel Luis reefs to Abrolhos Archipelago (areas included in our analysis as the group NBS-EBS).

The southern and south-eastern coastal reefs, cited by FLOETER et al. (2001) show lower mean annual water temperature, relatively higher primary production and a large shelf width. The reef-fish fauna living in this area appears to be the richest of Brazil, due to the mix of tropical and subtropical elements. The area is subjected to a relatively intense seasonal upwelling promoted by the South Atlantic Central Water, bringing low-temperature (<18°C) and nutrient-rich waters close to the coastline (EKAU & KNOPPERS 1999). FLOETER et al. (2001) stated that a considerable number of Caribbean reef fishes found in this region are absent from the north-eastern sites. We found a similar pattern in opisthobranchs. The cluster analysis groups ACR-SBB closer to the Caribbean provinces than to other Brazilian zones. On the other hand, ACR and SBB are the Brazilian areas with the highest richness in opisthobranchs. This could be related with environmental features (as is observed for reef-fishes; FLOETER et al. 2001). Nevertheless, in addition to environmental factors, differences in the richness of opisthobranchs for each area may depend upon other factors, such as discrepancies in sampling effort. The fauna from Brazil is better known in the South Brazilian Bight and Abrolhos-Campos zone, where Eveline and Ernst Marcus conducted research for over 30 years.

The north-eastern region as is described by Floeter et al. (2001) for fishes, which nearly overlap with the group NBS-EBS, is characterised by its relatively warm waters, a weak seasonal signal and a small vertical temperature gradient; the circulation is influenced northward by the North Brazilian Current, and southward by the Brazilian Current (Castro & Miranda 1998). The reef formation consists of coralline algal crusts over a rocky substrate, hermatypic and fire corals, as well as sponges (Floeter et al. 2001). The narrow and open shelf is an oligotrophic system almost entirely covered by carbonate sediments due to little freshwater input and the coast is influenced by the South Equatorial Current (Knoppers et al. 1999). In these areas herbivorous Sacoglossa and Anaspidea are more abundant. This trend of an increase in abundance in herbivores towards the tropical zone was previously observed in the Brazilian reef fishes (Ferreira et al. 2004).

With regard to the distribution of opisthobranch species, it can be noted that for each locality considered in this study, the percentage of species that extend northward is higher than southward. Several authors discussed the Southern Caribbean as a centre of origin of species (see Briggs 2006) from which the species have been penetrating northward into Florida and Bermudas and southward into Brazilian waters (Rocha 2003). Concerning Opisthobranchia, more intensive faunistic studies along the South American Atlantic coast are needed, before this hypothesis can be applied to understand opisthobranch diversity in that region.

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Table 1. Species checklists and geographical distribution.

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Acteocina atrata Mikkelsen & Mikkelsen, 1984	+	+	0	0	0	+	0	0	0	0	0	0	0	0
Acteocina bermudensis (Vanatta, 1901)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Acteocina bidentata (d'Orbigny, 1841)	+	+	+	+	0	+	0	+	+	+	+	+	+	+
Acteocina bullata (Kiener, 1834)	+	+	+	0	0	+	+	+	0	0	+	0	0	0
Acteocina canaliculata (Say, 1826)	+	+	+	0	0	0	0	0	0	0	0	0	0	0
Acteocina candei (d'Orbigny, 1841)	+	+	+	+	0	+	+	+	+	0	+	+	+	+
Acteocina decurrens (Verrill & Bush, 1900)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Acteocina inconspicua Olsson & McGinty, 1958	+	+	+	0	+	+	0	0	0	0	0	0	0	0
Acteocina kristenseni Jong & Coomans, 1988	0	0	0	0	+	0	0	0	0	0	0	0	0	0
Acteocina lepta Woodring, 1928	+	+	+	0	0	+	+	0	0	0	0	0	0	0
Acteocina liratispira (E. A. Smith, 1872)	0	0	0	0	0	0	0	+	0	0	+	0	0	0
Acteocina parviplica (Dall, 1894)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Acteocina perplicata (Dall, 1889)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Acteocina recta (d'Orbigny, 1841)	+	+	+	0	0	+	0	0	0	+	0	0	0	0
Acteon biplicatus (Strebel, 1908)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Acteon candens Rehder, 1939	+	+	+	0	0	+	0	0	0	0	+	0	0	0
Acteon danaida Dall, 1881	+	0	0	0	0	0	0	0	+	0	0	0	0	0
Acteon delicatus Dall, 1889	0	+	0	0	0	+	0	0	0	0	0	0	0	0
Acteon exiguus Mörch, 1875	0	0	+	+	0	+	0	0	0	0	0	0	0	0
Acteon finlayi McGinty, 1955	+	0	+	0	0	+	0	0	0	0	0	0	0	0
Acteon incisus Dall, 1881	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Acteon melampoides Dall, 1881	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Acteon pelecais Marcus, 1972	0	0	0	0	0	0	0	+	+	0	+	+	+	0
Acteon perforatus Dall, 1881	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Acteon splendidulus Mörch, 1875	0	0	0	+	+	+	0	0	0	0	0	0	0	0
Acteon vagabundus (Mabille & Rocgebrune, 1885)	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Aglaja felis Marcus & Marcus, 1970	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Aglaja hummelincki Marcus & Marcus, 1970	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Aglaja quinza Marcus, 1979	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Aglaja unsa Marcus & Marcus, 1969	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Atys alayoi Espinosa & Ortea, 2004	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Atys caribaeus (d'Orbigny, 1841)	+	+	+	0	0	+	0	0	+	0	0	0	0	0
Atys guildingi Sowerby II, 1869	0	0	+	0	0	+	0	0	+	0	0	0	0	0
Atys macandrewii E. A. Smith, 1872	0	+	+	0	+	+	0	0	+	0	0	0	0	0
Atys riiseanus Mörch, 1875	+	0	+	0	+	+	0	0	+	+	+	0	0	0
Atys sandersoni Dall, 1881	+	+	+	0	0	+	0	0	+	0	0	+	0	0
Atys sharpi Vanatta, 1901	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Bulla bermudae Verrill & Bush, 1900	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Bulla eburneola (Dall, 1927)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Bulla krebsii Dall, 1889	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Bulla nux Menke, 1853	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Bulla perstriata Menke, 1853	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Bulla pinguicula Seguenza, 1879	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Bulla solida Gmelin, 1791	+	+	+	0	0	+	0	0	0	0	0	0	0	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Bulla striata Bruguière, 1792	+	+	+	0	+	+	+	0	+	0	+	+	+	0
Bullina exquisita McGinty, 1955	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Bullina torrei (Aguayo & Rehder, 1936)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Chelidonura berolina Marcus & Marcus, 1970	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Chelidonura cubana Ortea & Martínez, 1997	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Chelidonura hirundinina (Quoy & Gaimard, 1833)	+	0	0	0	+	+	0	0	0	0	0	0	0	0
Chelidonura hummelincki Marcus & Marcus, 1970	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Chelidonura juancarlosi Ortea & Espinosa, 1998	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Chelidonura mariagordae Ortea, Espinosa & Moro, 2004	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Chelidonura petra Marcus, 1976	0	0	0	0	0	+	0	0	+	+	0	0	0	0
Chelidonura sabina Marcus & Marcus, 1970	+	+	0	0	+	0	0	0	0	0	0	0	0	0
Crenilabium exile (Jeffreys, 1870)	+	0	+	0	0	0	0	0	0	0	0	0	0	0
Cylichna alba (Brown, 1827)	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Cylichna auberii (d'Orbigny, 1841)	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Cylichna discus Watson, 1883	0	0	0	0	0	+	0	0	+	0	0	0	+	0
Cylichna eburnea A. E. Verrill, 1885	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylichna georgiana (Strebel, 1908)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Cylichna krebsii Mörch, 1875	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Cylichna verrillii Dall, 1889	+	0	0	0	0	0	0	0	0	0	0	0	+	0
Cylichna vortex (Dall, 1881)	+	+	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrobulla beauii P. Fischer, 1857	+	+	+	0	+	+	+	+	+	+	0	0	0	0
Cylindrobulla gigas Mikkelsen, 1998	+	+	+	0	0	+	+	0	0	0	0	0	0	0
Diaphana caribaea Espinosa, Ortea & Fernández-Garcés, 2001	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Diaphana seguenzae (Watson, 1886)	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Gastropteron chacmol Gosliner, 1989	+	+	+	0	0	+	0	0	0	0	0	+	0	0
Gastropteron hamanni Gosliner, 1989	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Gastropteron rubrum (Rafinesque, 1814)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Gastropteron vespertilium Gosliner & Armes, 1984	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Haminoea antillarum (d'Orbigny, 1841)	+	+	+	0	0	+	+	0	+	0	0	0	0	0
Haminoea elegans (Gray, 1825)	+	+	+	0	+	+	+	0	+	+	+	+	+	0
Haminoea glabra (A. Adams, 1850)	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Haminoea petitii (d'Orbigny, 1841)	0	+	+	0	+	+	0	0	+	0	0	0	0	0
Haminoea solitaria (Say, 1822)	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Haminoea succinea (Conrad, 1846)	+	+	+	0	0	+	+	0	0	0	0	0	0	0
Hydatina vesicaria (Lightfoot, 1786)	+	+	+	+	0	+	+	0	+	+	0	0	0	0
Japonacteon pusillus (Forbes, 1844)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Micromelo undatus (Bruguière, 1792)	+	0	+	0	+	+	+	0	+	+	0	0	0	0
Mysouffa cumingii (A. Adams, 1855)	+	0	0	0	0	0	0	0	0	+	+	+	+	0
Mysouffa turrita (Watson, 1883)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Navanax aenigmaticus (Bergh, 1893)	+	0	+	0	+	+	0	0	0	0	+	+	0	0
Navanax orbygnianus (Rochebrunne, 1881)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Ovulactaeon meekii Dall, 1889	0	0	0	0	0	+	0	0	+	0	0	0	0	0
Philine alba Mattox, 1958	0	0	+	0	0	0	0	0	0	0	0	0	+	0
Philine argentina Carcelles, 1947	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Philine caballeri Ortea, Espinosa & Moro, 2001	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Philine candeana (d'Orbigny, 1841)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Philine falklandica A. W. B. Powell, 1951	0	0	0	0	0	0	0	0	0	0	0	0	+	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Philine finmarchica M. Sars, 1859	0	0	0	+	0	+	0	0	0	0	0	0	0	0
Philine flexuosa M. Sars, 1870	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Philine infundibulum Dall, 1889	0	0	+	0	0	+	0	+	0	0	0	0	0	0
Philine mera Marcus & Marcus, 1969	0	0	0	0	0	0	0	0	0	0	+	+	+	0
Philine planata Dall, 1889	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Philine sagra (d'Orbigny, 1841)	+	0	+	0	0	+	0	+	+	+	0	0	0	0
Philine thurmanni Marcus & Marcus, 1969	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Philine trachyostraca Watson, 1897	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Philinopsis aeci Ortea & Espinosa, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Philinopsis pusa (Marcus & Marcus, 1966)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Pluscula cuica Marcus, 1953	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Pyrunculus caelatus (Bush, 1885)	+	+	+	+	0	+	0	0	0	0	0	+	0	+
Pyrunculus obesiusculus (Brugnone, 1877)	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Pyrunculus ovatus (Jeffreys, 1871)	+	0	0	0	0	+	0	0	+	0	0	0	0	0
Retusa canaliculata Wells & Wells, 1962	0	0	0	0	0	0	0	0	+	0	0	+	0	0
Retusa domita (Dall, 1889)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Retusa frielei (Dall, 1881)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Retusa omphalis Mörch, 1875	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Retusa pervia (Dall, 1889)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Retusa sosa Marcus & Marcus, 1969	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Retusa spatha (Watson, 1883)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Retusa sulcata (d'Orbigny, 1841)	+	+	+	0	0	+	0	0	0	0	0	0	0	0
Rictaxis punctostriatus (C. B. Adams, 1840)	+	+	+	0	0	+	+	0	0	0	0	0	0	0
Ringicula nitida A. E. Verrill, 1872	0	+	0	0	0	+	+	0	0	0	0	0	0	0
Ringicula semistriata d'Orbigny, 1842	+	+	+	0	0	+	0	0	0	0	0	0	0	0
Runcina divae (Marcus & Marcus, 1963)	+	0	+	0	+	+	+	0	0	0	+	0	0	0
Runcina inconspicua A. E. Verrill, 1901	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Runcina prasina (Mörch, 1863)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Scaphander bathymophila (Dall, 1881)	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Scaphander darius Marcus & Marcus, 1967	0	0	+	0	0	0	0	+	0	+	0	0	0	0
Scaphander loisae Bullis, 1956	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Scaphander nobilis A. E. Verrill, 1884	0	+	0	0	0	+	0	0	0	0	0	+	+	0
Scaphander pilsbryi McGinty, 1955	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Scaphander punctostriatus (Mighels & Adams, 1842)	0	+	+	0	0	+	0	0	0	0	0	0	0	0
Scaphander watsoni Dall, 1881	+	+	+	0	0	+	0	0	0	0	0	0	0	0
Toledonia bullata (Gould, 1847)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Volvulella minuta (Bush, 1885)	+	+	+	0	0	+	0	0	0	0	0	0	0	0
Volvulella paupercula (Watson, 1883)	+	+	0	0	0	+	0	0	0	0	0	0	+	0
Volvulella persimilis (Mörch, 1875)	+	+	+	+	0	+	+	0	+	0	0	+	+	+
Volvulella recta (Mörch, 1875)	0	0	0	0	0	+	0	0	0	0	+	0	0	0
Volvulella texasiana Harry, 1967	0	+	+	0	0	0	0	0	0	0	0	0	0	0
Alderia modesta (Loven, 1844)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Aplysiopsis formosa Pruvot-Fol, 1953	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Ascobulla ulla (Marcus & Marcus, 1970)	+	+	+	0	0	+	+	0	+	0	+	+	0	0
Berthelinia caribbea Edmunds, 1963	+	0	+	0	0	+	0	0	+	0	0	0	0	0
Bosellia corinneae Marcus, 1973	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Bosellia marcusi Marcus, 1972	+	0	+	0	0	+	0	0	0	0	0	0	0	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Bosellia mimetica Trinchese, 1891	+	0	0	0	+	+	+	0	0	+	0	0	0	0
Caliphylla mediterranea A. Costa, 1867	+	0	0	0	+	+	0	0	+	0	0	+	0	0
Costasiella lilianae Marcus, 1969	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Costasiella nonatoi Marcus & Marcus, 1960	+	0	0	0	0	+	0	0	0	0	0	+	0	0
Costasiella ocellifera (Simroth, 1895)	+	0	+	0	0	+	+	0	0	0	0	+	0	0
Cyerce antillensis Engel, 1927	+	0	0	0	+	+	+	0	0	0	0	0	0	0
Cyerce cristallina (Trinchese, 1881)	+	0	0	0	+	+	+	0	0	0	0	0	0	0
Cyerce edmundsi Thompson, 1977	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Cyerce habanensis Ortea & Templado, 1989	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Elysia canguzua Marcus, 1955	+	0	0	0	0	0	0	0	0	0	0	+	0	0
Elysia catulus (Gould, 1870)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Elysia cauze Marcus, 1957	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Elysia chitwa Marcus, 1955	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Elysia chlorotica Gould, 1870	+	+	0	0	0	0	0	0	0	0	0	0	0	0
Elysia cornigera Nuttall, 1989	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Elysia eugeniae Ortea & Espinosa, 2002	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Elysia evelinae Marcus, 1957	+	0	+	0	0	0	0	0	0	0	0	+	0	0
Elysia flava A. E. Verrill, 1901	0	0	+	0	0	+	+	0	+	0	0	0	0	0
Elysia nisbeti Thompson, 1977	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Elysia ornata (Swainson, 1840)	+	0	+	0	+	+	+	0	+	0	0	0	0	0
Elysia papillosa A. E. Verrill, 1901	+	0	+	0	+	+	+	0	0	0	0	0	0	0
Elysia patagonica Muniain & Ortea, 1997	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Elysia patina Marcus, 1980	+	0	+	0	0	+	0	0	0	0	0	0	0	0
Elysia pratensis Ortea & Espinosa, 1996	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Elysia purchoni Thompson, 1977	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Elysia serca Marcus, 1955	+	+	0	0	+	+	0	0	0	0	0	+	0	0
Elysia subornata A. E. Verrill, 1901	+	0	0	0	+	+	+	0	0	0	0	+	0	0
Elysia tuca Marcus & Marcus, 1967	+	0	+	0	+	+	+	0	+	+	+	0	0	0
Elysia zuleicae Ortea & Espinosa, 2002	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Ercolania cricetus (Marcus & Marcus, 1970)	+	0	+	0	+	+	0	0	0	0	0	0	0	0
Ercolania funerea (A. Costa, 1867)	+	+	0	0	+	+	0	0	0	0	0	0	0	0
Ercolania fuscata (Gould, 1870)	+	0	0	0	+	+	0	0	0	0	0	+	0	0
Ercolania selva Ortea & Espinosa, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Hermaea bifida (Montagu, 1815)	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Hermaea coirala Marcus, 1955	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Hermaea cruciata Gould, 1870	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Lobiger souverbii Fischer, 1857	+	+	+	0	+	+	0	0	0	0	0	+	0	0
Mourgona germaineae Marcus & Marcus, 1970	+	0	+	0	0	+	0	0	0	0	0	0	0	0
Mourgona murca Marcus & Marcus, 1970	0	0	0	0	+	0	0	0	0	0	0	0	0	0
Oxynoe aguayoi Jaume, 1945	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Oxynoe antillarum Mörch, 1863	+	+	+	0	+	+	+	0	+	+	+	+	0	0
Oxynoe azuropunctata Jensen, 1980	+	0	+	0	0	+	0	0	0	0	0	0	0	0
Oxynoe panamensis Pilsbry & Olsson, 1943	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Phyllobranchillus viridis (Deshayes, 1857)	+	0	+	0	+	+	0	0	0	0	0	0	0	0
Placida dendritica (Alder & Hancock, 1843)	0	0	0	0	+	0	0	0	0	0	0	0	0	0
Placida kingstoni Thompson, 1977	+	+	+	0	0	+	0	0	0	0	0	0	0	0
Placida verticilata Ortea, 1981	+	0	+	0	0	0	0	0	0	0	0	0	0	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Stiliger fuscovittatus Lance, 1962	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Stiliger talis Marcus, 1856	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Stiliger vanellus (Marcus, 1957)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Stiliger vossi Marcus & Marcus, 1960	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Thuridilla mazda Ortea & Espinosa, 2000	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Thuridilla picta (A. E. Verrill, 1901)	+	0	0	0	+	+	+	0	0	0	0	0	0	0
Tridachia crispata (Mörch, 1863)	+	+	+	0	+	+	+	0	0	0	0	0	0	0
Tridachia schrammi (Mörch, 1863)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Volvatella bermudae Clark, 1982	+	0	+	0	0	0	+	0	0	0	0	0	0	0
Akera bayeri Marcus & Marcus, 1967	+	0	+	0	0	0	0	0	+	0	0	0	0	0
Aplysia cervina (Dall & Simpson, 1901)	+	0	+	0	+	+	0	0	+	0	0	+	0	0
Aplysia dactylomela Rang, 1828	+	+	+	0	+	+	+	0	+	+	+	+	0	0
Aplysia fasciata Poiret, 1789	+	+	+	0	+	+	+	0	0	0	+	+	0	0
Aplysia geographica (Adams & Reeve, 1850)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Aplysia juliana Quoy & Gaimard, 1832	+	0	0	0	+	+	0	0	+	0	0	+	0	0
Aplysia morio (Verrill, 1901)	+	+	0	0	0	0	+	0	0	0	0	0	0	0
Aplysia parvula Mörch, 1863	0	+	+	0	+	+	+	0	+	+	+	0	0	0
Aplysia willcoxi Heilprin, 1887	+	+	0	0	0	+	+	0	0	0	0	0	0	0
Bursatella leachii Blainville, 1817	+	+	+	0	+	+	+	0	+	+	+	+	+	0
Dolabrifera dolabrifera (Rang, 1828)	+	0	+	+	+	+	+	0	0	0	+	0	0	0
Notarchus punctatus Philippi, 1836	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Petalifera petalifera (Rang, 1828)	0	0	0	0	+	+	0	0	0	+	0	0	0	0
Petalifera ramosa Baba, 1959	+	0	+	0	0	+	0	0	0	0	0	0	0	0
Phyllaplysia engeli Marcus, 1955	+	+	+	0	+	+	0	0	+	+	0	+	0	0
Phyllaplysia smaragda Clark, 1977	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Stylocheilus citrinus (Rang, 1828)	0	0	0	0	0	0	0	0	+	0	0	+	0	0
Stylocheilus longicauda (Quoy & Gaimard, 1824)	0	0	0	0	0	+	0	0	+	0	0	+	0	0
Stylocheilus striatus (Quoy & Gaimard, 1832)	+	0	+	0	+	+	+	0	+	+	+	0	0	0
Berthella agassizii (MacFarland, 1909)	0	0	+	0	+	0	+	0	+	0	+	+	0	0
Berthella patagonica (d'Orbigny, 1835)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Berthella stellata (Risso, 1826)	+	0	+	0	0	+	0	0	+	0	+	+	0	0
Berthella tamiu Marcus, 1984	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Berthellina circularis (Mörch, 1863)	0	0	0	0	0	+	0	0	+	0	0	0	0	0
Berthellina quadridens (Mörch, 1863)	0	0	+	0	0	+	0	0	+	+	0	0	0	0
Pleurobranchaea agassizii Bergh, 1897	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Pleurobranchaea inconspicua Bergh, 1897	+	+	+	+	0	+	0	0	+	+	+	+	+	+
Pleurobranchaea obesa (Verrill, 1882)	0	+	0	0	0	+	0	0	0	0	0	0	0	0
Pleurobranchaea tarda Verrill, 1880	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Pleurobranchus areolatus Mörch, 1863	+	+	+	0	+	+	+	0	+	0	0	+	0	0
Pleurobranchus emys Marcus, 1984	0	0	+	0	0	0	0	0	+	0	0	0	0	0
Pleurobranchus evelinae Thompson, 1977	0	0	0	0	0	+	0	0	+	0	0	0	0	0
Pleurobranchus iouspi Marcus, 1984	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Pleurobranchus lacteus Dall & Simpson, 1901	0	0	0	0	+	+	0	0	0	0	0	0	0	0
Pleurobranchus niveus (Verrill, 1901)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Tylodina americana Dall, 1890	0	+	0	0	0	+	+	0	0	0	0	0	0	0
Umbraculum umbraculum (Lightfoot, 1786)	+	+	+	0	0	+	+	+	+	+	0	0	0	0
Aegires absalaoi García, Troncoso & Domínguez, 2002	0	0	0	0	0	0	0	0	+	0	0	0	0	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Aegires gomezi Ortea, Luque & Templado, 1990	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Aegires ortizi Templado, Luque & Ortea, 1987	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Aegires sublaevis Odhner, 1932	0	0	+	0	0	0	+	0	0	0	0	0	0	0
Ancula espinosai Ortea, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Aphelodoris antillensis Bergh, 1879	+	0	+	0	+	+	+	0	0	0	0	0	0	0
Aporodoris millegrana (Alder & Hancock, 1854)	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Atagema browni Thompson, 1980	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Atagema hispida (d'Orbigny, 1837)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Atagema prea (Marcus & Marcus, 1967)	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Cadlina rumia Marcus, 1955	+	0	+	0	+	+	0	0	0	0	+	+	0	0
Cadlina scabriuscula (Bergh, 1890)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Cadlina sparsa (Odhner, 1921)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Ceratophyllidia papilligera (Bergh, 1890)	0	+	+	0	0	+	0	+	+	0	0	0	0	0
Chromodoris binza Marcus & Marcus, 1963	0	0	0	0	+	+	0	0	0	0	+	0	0	0
Chromodoris clenchi (Russell, 1935)	+	+	+	0	0	+	+	0	+	0	+	+	0	0
Chromodoris dictya Marcus & Marcus, 1970	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Chromodoris grahami Thompson, 1980	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Chromodoris kempfi Marcus, 1971	0	0	+	0	0	0	0	0	+	0	0	0	0	0
Chromodoris neona (Marcus, 1955)	0	0	0	0	0	0	0	0	0	0	+	+	0	0
Chromodoris perola Marcus, 1976	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Chromodoris ponga Marcus & Marcus, 1970	0	0	0	0	+	0	0	0	0	0	0	0	0	0
Chromodoris punctilucens Bergh, 1890	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Chromodoris roseopicta Verrill, 1900	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Corambe evelinae Marcus, 1958	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Corambe obscura A. E. Verrill, 1870	0	+	0	0	0	+	0	0	0	0	0	+	0	0
Dendrodoris krebsii (Mörch, 1863)	+	+	+	0	+	+	0	0	0	0	+	+	0	0
Dendrodoris magagnai Ortea & Espinosa, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Dendrodoris senegalensis Bouchet 1977	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Dendrodoris warta Marcus & Gallagher, 1976	+	+	0	0	0	0	0	0	0	0	0	0	0	0
Diaulula greeleyi (MacFarland, 1909)	0	0	+	0	0	+	0	0	+	+	+	+	0	0
Diaulula punctuolata (d'Orbigny, 1837)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Diaulula worki (Marcus & Marcus, 1967)	+	0	0	0	+	0	0	0	0	0	0	0	0	0
Discodoris alba White, 1952	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Discodoris branneri MacFarland, 1909	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Discodoris evelinae Marcus, 1955	+	+	+	0	0	+	0	0	+	0	+	+	0	0
Discodoris mortenseni Marcus & Marcus, 1963	+	0	+	0	+	+	0	0	0	0	0	0	0	0
Discodoris muta Bergh, 1877	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Discodoris notha Bergh, 1877	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Discodoris ketos gila (Marcus & Marcus, 1970)	0	0	0	0	+	0	0	0	0	0	0	0	0	0
Discodoris phoca Marcus & Marcus, 1967	+	0	+	0	0	0	0	0	+	0	0	0	0	0
Discodoris purcina Marcus & Marcus, 1967	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Discodoris voniheringi MacFarland, 1909	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Doridella carambola (Marcus, 1955)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Doriopsilla areolata nigrolineata Meyer, 1977	0	0	+	0	0	0	0	0	0	0	0	+	0	0
Doriopsilla espinosai Valdés & Ortea, 1998	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Doriopsilla pharpa Marcus, 1961	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Doris bicolor (Bergh, 1884)	+	0	0	0	0	0	0	0	0	0	0	0	0	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Doris bovena Marcus, 1955	0	0	0	0	+	0	0	0	0	0	0	+	0	0
Doris fontainei d'Orbigny, 1837	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Doris fretterae Thompson, 1980	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Doris ilo (Marcus, 1955)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Doris kerguelenensis (Bergh, 1884)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Doris kyolis (Marcus & Marcus, 1967)	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Doris pickensi Marcus & Marcus, 1967	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Doris verrucosa Linné, 1758	+	+	+	0	0	0	0	0	+	0	+	+	0	0
Etidoris ladislavii Ihering, 1886	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Galacera marplatensis (Franceschi, 1928)	0	0	0	0	0	0	0	0	0	0	0	+	0	+
Gargamella immaculata Bergh, 1894	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Geitodoris patagonica Odhner, 1926	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Geitodoris planata (Alder y Hancock, 1846)	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Geitodoris pusae (Marcus, 1955)	+	0	0	0	+	+	0	+	0	0	0	+	0	+
Geitodoris immunda Bergh, 1894	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Glossodoris moerchi (Bergh, 1879)	0	+	0	0	0	+	0	0	0	0	0	0	0	0
Glossodoris sedna (Marcus & Marcus, 1967)	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Goniodoris mimula Marcus, 1955	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Hallaxa apefae Marcus, 1957	0	0	0	0	0	0	0	0	0	0	+	+	0	0
Hexabranchus morsomus Marcus & Marcus, 1962	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Holoplocamus papposus Odhner, 1926	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Hoplodoris hansrosaorum Dominguez, Garcia & Troncoso, 2006	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Hypselodoris acriba Marcus & Marcus, 1967	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Hypselodoris bayeri (Marcus & Marcus, 1967)	+	0	+	0	0	+	0	0	0	0	0	0	0	0
Hypselodoris espinosai Ortea & Valdés, 1996	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Hypselodoris lajensis Troncoso, Garcia & Urgorri, 1998	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Hypselodoris marci Marcus, 1971	0	0	+	0	0	+	0	0	0	0	+	0	0	0
Hypselodoris picta (Schultz, 1836)	+	+	0	0	0	0	0	0	0	0	0	+	0	0
Hypselodoris ruthae Marcus & Hughes, 1974	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Hypselodoris sycilla (Bergh, 1890)	+	0	+	0	0	+	0	0	+	0	0	0	0	0
Hypselodoris zebra (Heilprin, 1888)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Jorunna spazzola (Marcus, 1955)	0	0	0	0	0	+	0	0	0	+	+	+	0	0
Kankelibranchus incognitus Ortea, Espinosa & Caballer, 2005	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Lophodoris scala Marcus & Marcus, 1970	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Mexichromis molloi Ortea & Valdés, 1996	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Noumea regalis Ortea, Caballer & Moro, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Okenia impexa Marcus, 1957	0	0	0	0	0	+	0	0	0	0	0	+	0	0
Okenia miramarae Ortea & Espinosa, 2000	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Okenia zoobotryon (Smallwood, 1910)	+	0	0	0	0	+	+	0	0	0	+	+	0	0
Onchidoris aureopuncta (Verrill, 1901)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Onchidoris bilamellata (Linné, 1761)	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Onchidoris lactea (Verrill, 1900)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Onchidoris miniata (Verrill, 1901)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Onchidoris olivacea (Verrill, 1900)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Onchidoris quadrimaculata (Verrill, 1900)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Paradoris mulciber (Marcus, 1971)	0	0	+	0	0	0	0	0	+	0	0	0	0	0
Peltodoris crucis (Mörch, 1863)	0	0	0	0	0	+	0	0	0	0	0	0	0	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Peltodoris hummelincki Marcus & Marcus, 1963	0	0	+	0	+	0	0	0	0	0	0	0	0	0
Phyllidiella molaensis (Meyer, 1977)	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Platydoris angustipes (Mörch, 1863)	+	0	+	0	0	+	0	0	+	0	+	0	0	0
Plocamopherus gulo Marcus, 1979	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Plocamopherus lucayensis Hamann & Farmer, 1988	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Plocamopherus pilatectus Hamann & Farmer, 1988	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Polycera aurisula Marcus, 1957	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Polycera hedgpethi Marcus, 1964	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Polycera herthae Marcus & Marcus, 1963	0	0	0	0	+	+	0	0	0	0	0	0	0	0
Polycera hummi Abbott, 1952	+	+	0	0	0	0	0	0	0	0	0	0	0	0
Polycera japonica Baba, 1949	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Polycera manzanilloensis Ortea, Espinosa & Camacho, 1999	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Polycera odhneri Marcus, 1955	+	0	0	0	+	+	0	0	0	0	0	+	0	0
Polycera quadrilineata (Müller, 1776)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Polycera rycia Marcus & Marcus, 1970	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Polycerella emertoni Verrill, 1880	+	0	+	0	0	+	0	0	0	0	0	+	0	0
Risbecia nyalya (Marcus & Marcus, 1967)	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Rostanga byga Marcus, 1958	0	0	0	0	0	0	0	0	+	0	0	+	0	+
Rostanga pulchra MacFarland, 1905	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Siraius ilo Marcus, 1955	0	0	0	0	0	0	0	0	0	0	+	+	0	0
Siraius kyolis Marcus & Marcus, 1967	0	0	0	0	0	0	0	0	+	0	+	0	0	0
Tambja divae (Marcus, 1958)	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Tambja gratiosa (Bergh, 1890)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Tambja oliva Meyer, 1977	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Tambja stegosauriformis Pola, Cervera & Gosliner, 2005	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Taringa millegrana (Alder & Hancock, 1855)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Taringa telopia Marcus, 1955	+	0	+	0	0	+	0	0	0	0	+	+	0	0
Taringa tritorquis Ortea, Pérez & Llera, 1982	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Thecacera pennigera (Montagu, 1815)	+	0	0	0	0	0	0	0	0	0	0	+	0	0
Thordisa diuda Marcus, 1955	0	0	0	0	0	+	0	0	+	0	0	+	0	0
Thordisa lurca (Marcus & Marcus, 1967)	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Trapania dalva Marcus, 1972	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Trapania maringa Marcus, 1957	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Trippa anceps (Bergh, 1890)	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Tyrinna evelinae (Marcus, 1958)	0	0	+	0	0	+	0	0	0	0	+	+	0	0
Tyrinna nobilis Bergh, 1898	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Bornella calcarata Mörch, 1863	0	0	+	+	0	+	0	0	+	0	0	0	0	0
Doto awapa Ortea, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Doto cabecar Ortea, 2001	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Doto caramella Marcus, 1957	0	0	0	0	+	0	0	0	0	0	0	+	0	0
Doto chica Marcus & Marcus, 1960	+	+	+	0	+	+	0	0	0	0	0	0	0	0
Doto curere Ortea, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Doto divae Marcus & Marcus, 1960	+	0	0	0	+	0	0	0	+	+	0	0	0	0
Doto duao Ortea, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Doto escatllari Ortea, Moro & Espinosa, 1999	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Doto iugula Ortea, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Doto kekoldi Ortea, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Doto pita Marcus, 1955	+	0	0	0	+	+	0	0	0	0	0	+	0	0
Doto proranao Ortea, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Doto pygmaea Bergh, 1871	0	0	0	0	0	+	+	0	0	0	0	0	0	0
Doto sabuli Ortea, 2001	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Doto uva Marcus, 1955	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Doto varaderoensis Ortea, 2001	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Hancockia ryrca Marcus, 1957	0	0	0	0	+	+	0	0	0	0	0	+	0	0
Lomanotus phiops Marcus, 1957	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Lomanotus vermiformis Eliot, 1908	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Marionia cucullata (Gould, 1852)	0	0	+	0	0	0	0	0	0	0	0	+	0	+
Marionia tedi Marcus, 1983	+	0	+	0	0	+	0	0	0	0	0	0	0	0
Miesea evelinae (Marcus, 1957)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Scyllaea pelagica Linné, 1758	+	+	+	0	+	+	+	0	+	0	0	0	0	0
Phylliroe atlantica Bergh, 1871	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Phylliroe bucephala Lamarck, 1816	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Tethys occidentalis (Odhner, 1936)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Tritonia australis Bergh, 1898	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Tritonia bayeri Marcus & Marcus, 1967	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Tritonia eriosi Marcus, 1983	0	0	0	0	0	0	0	0	0	0	0	0	+	+
Tritonia hamnerorum Gosliner & Ghiselin, 1987	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Tritonidoxa wellsi (Marcus, 1961)	+	0	+	0	0	0	0	0	0	0	0	+	0	0
Tritoniopsis frydis Marcus & Marcus, 1970	+	0	0	0	0	+	+	0	0	0	0	0	0	0
Armina elongata Ardila & Valdés, 2004	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Armina juliana Ardila & Díaz, 2002	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Armina muelleri (Ihering, 1886)	+	+	+	+	0	+	0	0	0	0	+	+	0	0
Janolus comis Marcus, 1955	+	0	0	0	+	0	0	0	0	0	0	+	0	0
Janolus costacubensis Ortea & Espinosa, 2000	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Janolus mucloc (Marcus, 1958)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Anteaeolidiella indica Bergh, 1888	+	0	0	0	+	+	0	0	0	0	+	+	0	0
Aeolidia serotina Bergh, 1873	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Aeolidiella occidentalis Bergh, 1875	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Anetarca brasiliana García & Troncoso, 2004	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Austraeolis catina Marcus & Marcus, 1967	+	0	0	0	0	+	0	0	0	0	0	0	0	0
Babakina festiva (Roller, 1972)	0	0	0	0	0	0	0	0	0	0	+	0	0	0
Berghia benteva (Marcus, 1958)	0	0	0	0	0	0	0	0	0	0	+	+	0	0
Berghia coerulescens (Laurillard in Cuvier, 1830)	0	0	0	0	+	+	0	0	0	0	0	0	0	0
Berghia creutzbergi Marcus & Marcus, 1970	0	0	+	0	+	+	0	0	0	0	+	0	0	0
Berghia verrucicornis (A. Costa, 1864)	+	0	+	0	0	+	0	0	0	0	0	0	0	0
Berghia rissodominguezi Muniain & Ortea, 1999	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Calmella bandeli Marcus, 1976	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Catriona maua Marcus & Marcus, 1960	+	0	0	0	+	+	0	0	0	0	0	0	0	0
Catriona oba Marcus, 1970	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Cerberilla tanna Marcus & Marcus, 1960	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Cratena pilata (Gould, 1870)	+	+	0	0	0	0	+	0	0	0	0	+	0	0
Cratena piutaensis Ortea, Caballer & Espinosa, 2003	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Cuthona barbadiana Edmunds & Just, 1983	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Cuthona caerulea (Montagu, 1804)	+	0	0	0	0	0	0	0	0	0	0	+	0	0

Species	CC-CR	CR-Cro	CRo-O	O-A	ABC	WI	BER	AS	NBS	EBS	ACR	SBB	SBS	ARG
Cuthona genovae (O'Donoghue, 1929)	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Cuthona georgiana (Pfeffer, 1886)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Cuthona iris Edmunds & Just, 1983	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Cuthona perca (Marcus, 1958)	+	0	+	0	0	+	0	0	0	0	0	+	0	0
Cuthona pumilio Bergh, 1871	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Cuthona rubra (Edmunds, 1964)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Cuthona tina (Marcus, 1957)	+	0	0	0	+	+	0	0	0	0	0	+	0	0
Dondice occidentalis (Engel, 1925)	+	0	+	0	+	+	0	0	0	0	0	+	0	0
Dondice parguerensis Brandon & Cutress, 1985	0	0	0	0	0	+	+	0	0	0	0	0	0	0
Eubranchus conicla (Marcus, 1958)	+	0	+	0	0	+	0	0	0	0	0	+	0	0
Eubranchus convenientis Ortea & Caballer, 2002	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Eubranchus leopoldoi Caballer, Ortea & Espinosa, 2001	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Eubranchus toledanoi Ortea & Caballer, 2002	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Facelina agari Smallwood, 1910	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Facelina coenda Marcus, 1958	0	0	0	0	0	0	0	0	0	0	+	+	0	0
Facelina goslingii A. E. Verrill, 1901	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Facelina karouae (Marcus, 1957)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Favorinus auritulus Marcus, 1955	+	0	0	0	+	+	+	0	0	0	0	+	0	0
Fiona pinnata (Eschscholtz, 1831)	0	+	0	0	+	0	+	0	0	0	0	0	0	+
Flabellina dushia (Marcus & Marcus, 1963)	0	0	0	0	+	0	0	0	0	0	+	0	0	0
Flabellina engeli Marcus & Marcus, 1968	+	0	+	0	+	+	0	0	0	0	+	+	0	0
Flabellina hamanni Gosliner, 1994	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Flabellina marcusorum Gosliner & Kuzirian, 1990	0	0	+	0	+	0	0	0	0	0	0	+	0	0
Flabellina pallida (Verrill, 1900)	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Flabellina verta (Marcus, 1970)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Glaucus atlanticus Forster, 1777	0	+	0	0	+	+	+	0	0	0	+	+	+	0
Godiva rubrolineata Edmunds, 1964	+	0	0	0	+	+	0	0	0	0	0	+	0	0
Learchis evelinae Edmunds & Just, 1983	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Learchis poica Marcus & Marcus, 1960	+	0	+	0	+	+	0	0	0	0	0	0	0	0
Limenandra nodosa Haefelfinger & Stamm, 1958	0	0	0	0	+	0	0	0	0	0	0	0	0	0
Millereolidia ritmica (Ortea, Caballer & Espinosa, 2003)	0	0	+	0	0	0	0	0	0	0	0	0	0	0
Nanuca sebastiani Marcus, 1957	0	0	+	0	+	+	0	0	0	+	0	+	0	0
Palisa kristenseni (Marcus & Marcus, 1963)	+	0	0	0	+	+	0	0	0	0	0	0	0	0
Pauleo jubatus Millen & Hamann, 1992	0	0	+	0	0	+	0	0	0	0	0	0	0	0
Phidiana lynceus Bergh, 1867	+	0	+	0	+	+	0	0	0	0	+	+	0	0
Phidiana patagonica (d'Orbigny, 1836)	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Phidiana riosi García & Troncoso, 2003	0	0	0	0	0	0	0	0	+	0	0	0	0	0
Piseinotecus divae Marcus, 1955	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Pseudovermis salamandrops Marcus, 1953	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Spurilla alba (Risbec, 1928)	0	0	0	0	0	+	0	0	0	0	0	0	0	0
Spurilla neapolitana (delle Chiaje, 1844)	+	+	+	0	+	+	+	0	+	0	+	+	0	0
Tenellia adspersa (Nordmann, 1845)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Tenellia fuscata (Gould, 1870)	+	0	0	0	0	0	0	0	0	0	0	0	0	0
Tenellia pallida (Alder & Hancock, 1855)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Tergipes despectus (Johnston, 1835)	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Tergipes tergipes (Forskål, 1775)	0	0	0	0	0	0	0	0	0	0	0	+	0	0

Table 2. Limits and features of the areas considered along Brazilian coasts, based on CASTRO & MIRANDA (1998).

Regions	Coastal Limits	Width of continental shelf (Km)	Shelf-breaks depth (m)	Currents	Salinity ($^{0}/_{00}$)	Temperature (°C)
Amazon Shelf (AS)	4°N–2°S	125–320	140	North Brazil Current Geostrophic Current Amazon River	<33	27
Northeastern Brazilian Shelf (NBS)	2°S–8°S	40–85	73	North Brazil Current	36–37	Summer: 27–29 Winter: 26-28
Eastern Brazilian Shelf (EBS)	8°S–15°S	10–15	50–60	South Equatorial Current	36-37 River 32-33	Summer: 27–28 Winter: 25–26
Abrolhos-Campos region (ACR)	15°S–23°S	35–190	60–100	Brazil Current South Atlantic Central Water Coastal Water Upwelling events	36.5-37	Summer: 25–27 Winter: 22–24 Upwelling: 16
South Brazilian Bight (SBB)	23°S–28.4°S	50–230	120–180	Brazil Current South Atlantic Central Water Fresh Coastal Water	<33->36	Summer: 25–27 Upwelling in North:21 Winter: 20–23 Water from South <18
Southern Brazilian Shelf (SBS)	28.5°S–34°S	110–170	180	Summer: Brazil Current Winter: Subantarctic Water	Summer: >36 Winter: <34	Summer: >20 Winter: <15

Table 3. Number of species by order or suborder for each area considered.

	CC-CR	CR-Cro	CRo-O	ABC	WI	BER	O-A	AS	NBS	EBS	ACR	SBB	SBS	Arg
Cephalaspidea	50	39	52	14	88	19	8	9	26	11	14	19	14	10
Sacoglossa	38	8	29	19	37	14	0	0	7	3	3	18	0	1
Anaspidea	14	7	11	10	14	8	1	0	10	6	6	8	1	0
Notaspidea	6	5	8	3	12	5	1	1	10	4	3	5	1	2
Doridina	35	12	39	13	52	11	0	2	17	2	23	36	0	14
Dendronotina	9	2	16	6	14	5	1	0	3	1	0	8	1	3
Arminina	3	1	4	1	2	0	1	0	0	0	1	2	0	0
Aeolidina	18	5	19	19	31	10	0	0	2	1	12	26	1	5
Total	173	79	178	85	250	72	12	12	75	28	62	122	18	35

Table 4. Percentage of species from each area (vertical column) present in other localities.

	CC-CR	CR-CRo	CRo-O	ABC	WI	Ber	O-A	AS	NBS	EBS	ABR	SBB	SBS	ARG	Total of species
CC-CR	100	34	53	34	73	25	5	4	24	11	19	34	6	3	173
CR-CRo	75	100	66	30	78	39	9	8	34	15	25	37	13	8	79
CRo-O	51	29	100	24	69	21	6	5	28	12	20	25	4	3	178
ABC	69	28	51	100	80	34	2	2	27	18	28	44	5	2	85
WI	50	25	49	27	100	19	5	4	21	10	16	24	4	2	250
BER	61	43	51	40	67	100	6	6	32	17	26	26	8	4	72
O-A	67	58	83	17	100	33	100	17	50	25	42	50	33	42	12
AS	58	50	75	17	75	33	17	100	58	42	42	33	25	25	12
NBS	55	36	65	31	69	31	8	9	100	28	31	39	12	7	75
EBS	68	43	75	54	86	43	11	18	75	100	46	39	18	7	28
ABR	53	32	58	39	65	31	8	8	37	21	100	61	16	5	62
SBB	48	24	36	30	48	16	5	3	24	9	31	100	10	7	122
SBS	56	56	44	22	61	33	22	17	50	28	56	67	100	28	18
ARG	17	17	17	6	17	9	14	9	14	6	9	26	14	100	35
Total of species	173	79	178	85	250	72	12	12	75	28	62	122	18	35	

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Paddle cilia on the cephalic sensory organs (CSOs) of Opisthobranchia (Mollusca: Gastropoda) – genuine structures or artefacts?*

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Abstract. Paddle cilia are characterised by a curved axoneme at the distal end enclosed by the ciliary membrane. They have been described in numerous different marine invertebrates including one species of Opisthobranchia. There is still controversy about the nature of paddle cilia. Various considerations have been made concerning their function regarding them as genuine structures, whereas other authors claimed paddle cilia to be artefacts. The current study focuses on investigating paddle cilia on the cephalic sensory organs (CSOs) of different opisthobranch species in order to present more data and perhaps clarify the paddle cilia discussion. For this purpose specimens were fixed using two different methods. One method comprises an isoosmotic fixation solution which did not induce paddle cilia formation in bivalve larvae (SHORT & TAMM 1991). The other method utilises a hypoosmotic fixation solution. Using scanning electron microscopy paddle cilia can be detected in all investigated species. The abundance of paddle cilia was lower in the majority of specimens fixed with the isoosmotic solution which led us to conclude that paddle cilia are indeed artefacts.

Keywords. Scanning Electron Microscopy, isoosmotic fixation.

1. INTRODUCTION

Paddle cilia or discocilia were first described by TAMARIN et al. (1974) as cilia whose cylindrical stem curves back upon itself and forms a 360° loop which is completely enveloped by the ciliary membrane. Since then paddle cilia have been discovered in many different marine invertebrates (EHLERS & EHLERS 1978; HEIMLER 1978; BONE et al. 1982; MATERA & DAVIS 1982; CAMPOS & MANN 1988).

Various considerations were made concerning the function of this special structure. TAMARIN et al. (1974) proposed that paddle cilia function as microscopic spatulas for the application of adhesive plaque material to substrate surfaces. HEIMLER (1978) supposed that they are locomotory organs since the disc shaped heads can be interpreted as enlargements of the surface to improve the efficiency of the ciliary beat. Thus paddle cilia also influenced the nutrition of the larvae investigated in his study. CAMPOS & MANN (1988) detected paddle cilia on the velum of bivalve larvae of two different species. They regarded them as genuine structures and favoured a locomotory and/or chemosensory function although they were not able to prove this assumption, since the occurrence of paddle cilia did not enhance the rate of movement in the examined species (CAMPOS & MANN 1988).

So far, only one study deals with the presence of paddle cilia in Opisthobranchia. The investigation of *Pleurobranchaea californica* revealed that paddle cilia solely occurred in chemosensitive regions of this species (DAVIS & MATERA 1982). This fact led DAVIS & MATERA (1982) to the conclusion that paddle cilia are most likely chemoreceptors. The dilatations were expected to enlarge the membrane surface area, increasing the opportunity for interaction with chemical substances.

Other authors supposed paddle cilia to be artefacts resulting from osmotic stress, increased temperature, non-physiological conditions or fixation (EHLERS & EHLERS 1978; BONE et al. 1982; NIELSEN 1987; SHORT & TAMM 1991; DEINER et al. 1993).

SHORT & TAMM (1991) discovered that the occurrence of paddle cilia is associated with the osmolarity of the fixation solution. After the application of an isoosmotic fixation solution with 50% seawater no paddle cilia could be detected in their bivalve larvae, whereas other hypoosmotic fixation solutions induced the formation of paddle cilia. However, the occurrence of paddle cilia was always restricted to certain areas and never affected all cilia of the larvae. NIELSEN (1987) argued that different cilia - even on the same organism - are not equally sensitive to stress and some cilia are indeed difficult to fix in a normal shape. DEINER et al. (1993) reported that paddle cilia induced by hypotonic solutions usually regain their normal appearance if specimens are returned to isotonic solutions.

The current study investigates the cilia on the cephalic sensory organs (CSOs) of different Opisthobranchia. CSOs are special structures in the head region of sea slugs, which are sensitive to several stimuli. The purpose of this investigation is to detect paddle cilia and clarify the question whether they are genuine structures or artefacts.

2. MATERIAL AND METHODS

Specimens of *Acteon tornatilis* (Linnaeus, 1758) (Acteonoidea), *Aeolidiella glauca* (Alder and Hancock, 1845) (Nudibranchia), *Aplysia punctata* Cuvier, 1803 (Anaspidea) and *Berthella plumula* (Montagu, 1803) (Pleurobranchoidea) were collected in the intertidal at Roscoff and Saint Michel-en-Grève (Brittany, France). *Haminoea hydatis* (Linnaeus, 1758) (Cephalaspidea) was obtained from a laboratory culture at the J.W.G.-University of Frankfurt.

We applied the isoosmotic fixation method of SHORT & TAMM (1991) and a hypoosmotic fixation solution in order to clarify the nature of paddle cilia on the cephalic sensory organs of different Opisthobranchia. The specimens were anaesthetised by an injection of 7% $MgCl_2$ in the foot and the CSOs were abscised. Two different methods have been applied: CSOs of investigated species were fixed in 2.5% glutaraldehyde, 1% paraformaldehyde in phosphate buffer, pH 7.2 – 7.4 at room temperature (method 1). The osmolarity of this solution was approximately 250 mOsmols less than the osmolarity of the isoosmotic fixation solution and the artificial seawater in which the specimens were cultivated (determined with the help of Knauer Semi-Micro Osmometer). Additional CSOs of *Acteon tornatilis*, *Aplysia punctata*, *Berthella plumula* and *Haminoea hydatis* were fixed in an isoosmotic solution after SHORT and TAMM (1991) containing 2.5% glutaraldehyde, 0.13 M NaCl and 50% seawater, pH 7.2 – 7.4 at room temperature (method 2). The investigated CSOs and number of

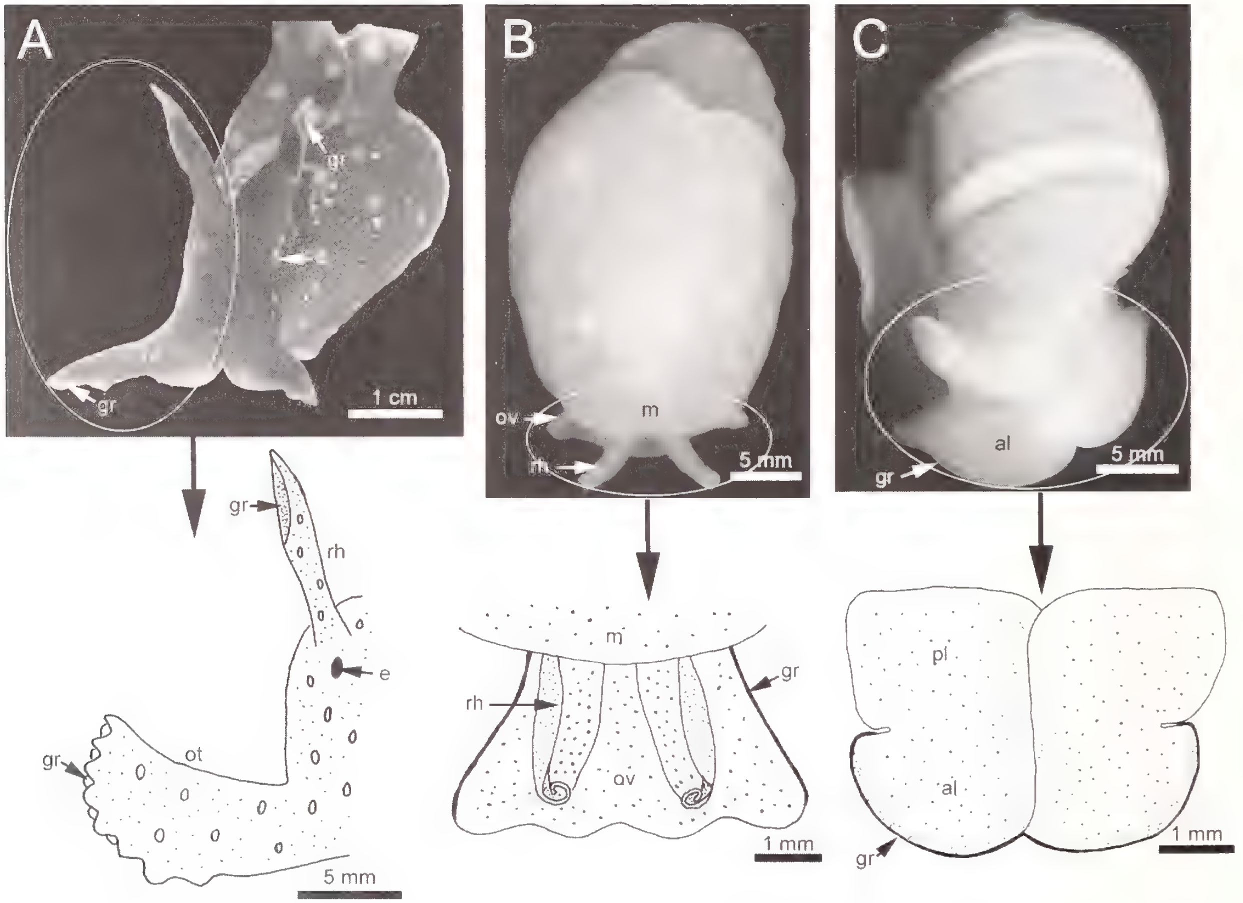

Fig. 1. Photographs of the investigated species and schematic drawings of their cephalic sensory organs (CSOs). **A** *Aplysia punctata*. **B** *Berthella plumula*. **C** *Acteon tornatilis*. al anterior lobe, e eye, gr groove, m mantle, ot oral tentacle, ov oral veil, pl posterior lobe, rh rhinophore.

replicates were as follows (method 1/ method 2): *Acteon tornatilis* head shield (4/1), *Aeolidiella glauca* rhinophore (2/-), oral tentacle (2/-), *Aplysia punctata* rhinophore (4/2), oral tentacle (4/2), *Berthella plumula* rhinophore (6/2), oral veil (3/1), *Haminoea hydatis* head shield (4/1), lip organ (4/2), Hancock´s organ (4/2).

For SEM, fixed CSOs were dehydrated through a graded acetone series, critical point dried (BAL-TEC, CPD 030), sputtered with gold (Sputter-Coater, Agar Scientific) and examined with a Hitachi S4500 SEM. Photographs were taken with DISS – Digital Image Scanning System (Point Electronic).

Sizes of cilia were determined by average over measurement of at least ten cilia.

3. RESULTS

The investigated species exhibit several different types of CSOs (Figs. 1 and 2), like rhinophore, oral tentacle, oral veil, head shield, lip organ and Hancock´s organ. The rhinophores and oral tentacles of *Aplysia punctata* (Fig. 1A) possess dark pigmented grooves. These grooves contain tufts of cilia. A total of four rhinophores fixed with method 1 were investigated. One of these exhibits paddle cilia (Fig. 3A), whereas the other reveal cilia without paddle shaped ends (Fig. 3B). The rhinophore exhibiting paddle cilia has a total length of 3 mm, whereas the other investigated rhinophores without paddle cilia are 5 mm long. The rhinophores fixed with method 2 show both cilia with and without paddle-shaped ends. The paddle cilia are always shorter (~12 µm) than the other cilia (~16 µm).

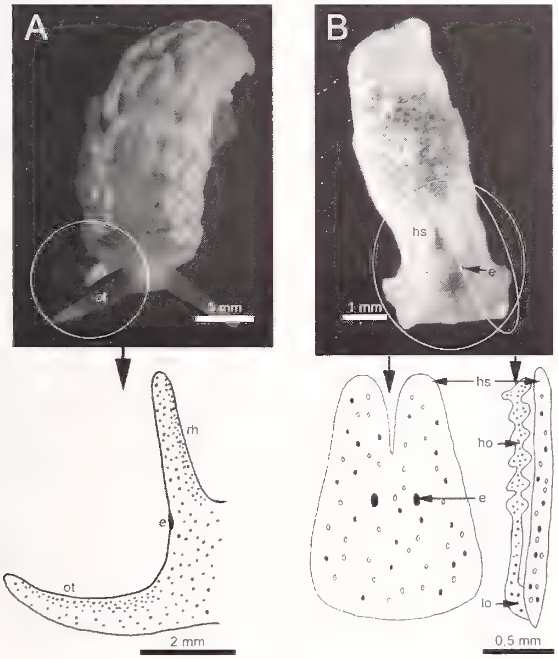

Fig. 2. Photographs of the investigated species and schematic drawings of their CSOs. **A** *Aeolidiella glauca.* **B** *Haminoea hydatis* – scheme: dorsal (left) and lateral (right) view of the CSOs. e eye, ho Hancock´s organ, hs head shield, lo lip organ, ot oral tentacle, rh rhinophore.

The oral tentacles fixed with method 1 reveal mainly paddle cilia (Fig. 3C) with a length of ~12 µm. Cilia without paddles are ~16 µm long (Fig. 3D). The oral tentacles fixed with method 2 possess mainly cilia without paddle-shaped ends (Fig. 3E), the fewer paddle cilia occur in single tufts.

Berthella plumula possesses rolled rhinophores and an oral veil with lateral grooves (Fig. 1B). Inside the rhinophores tufts of cilia are arranged regularly from the tip to the base of this CSO. These cilia have straight tips in rhinophores (Fig. 3F) fixed with method 1, whereas they reveal paddle-shaped ends in those preserved with method 2. Outside the rhinophores mainly paddle cilia are found (Fig. 3G) irrespective of fixation methods.

Inside the lateral grooves of the oral veils fixed with method 1 tufts of cilia with straight tips were found (Fig. 3H). On the margin of the grooves as well as on the dorsal and ventral side of the oral veil paddle cilia are predominant (Fig. 3I). The isoosmotically fixed oral veil also reveals paddle cilia inside the grooves.

The head shield of *Haminoea hydatis* possesses postero-lateral flattened appendages. The lip organ is located anteriorly beneath the head shield and continues into the Hancock´s organ. The arrangement of the three CSOs is shown in Fig. 2B. The lip organ reveals tufts of paddle cilia as well as tufts of cilia with straight tips and even both types of cilia in one tuft (Fig. 4A) after fixation with method 1. The Hancock´s organ also exhibits cilia with (Fig. 4B) and without paddle-shaped ends when fixed with method 1. In contrast to this, both CSOs showed no paddle cilia after fixation with method 2 (Fig. 4C and D). The head shield is densely covered by cilia on the dorsal side. No paddle cilia could be detected after application of both fixation methods. Nevertheless fixation with method 1 resulted in cilia whose tips are curved to the axoneme (Fig. 4E), whereas fixation with method 2 revealed cilia with straight tips (Fig. 4F).

The head shield of *Acteon tornatilis* is completely covered by cilia. It is divided into a pair of antero-lateral lobes and a pair of postero-lateral lobes (Fig. 1C). A groove runs along the front and lateral side of the anterior lobe. The specimens fixed with method 1 show numerous cilia with slightly, and some cilia with extremely, swollen ends in-

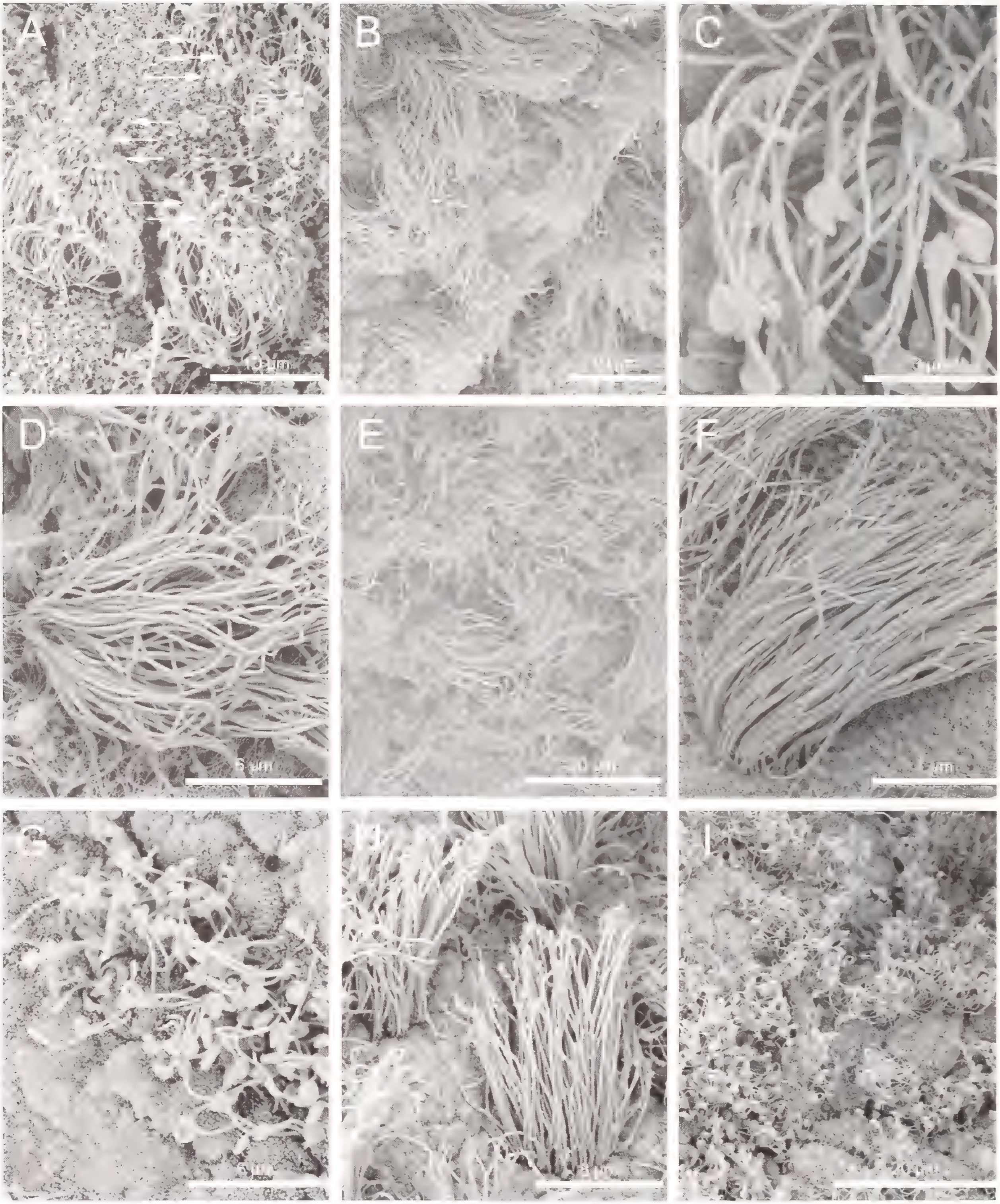

Fig. 3. Scanning electron microscopy of sensory regions of the CSOs of *Aplysia punctata* and *Berthella plumula* fixed with method 1 (except E). **A** rhinophore of *Aplysia punctata* – paddle cilia (arrows) inside the groove of a small individual. **B** rhinophore of *Aplysia punctata* – cilia inside the groove. **C** oral tentacle of *Aplysia punctata* – paddle cilia inside the groove. **D** oral tentacle of *Aplysia punctata* – tuft of cilia without paddle-shaped ends inside the groove. **E** oral tentacle of *Aplysia punctata* fixed with method 2 – cilia inside the groove. **F** rhinophore of *Berthella plumula* – cilia on the inside. **G** rhinophore of *Berthella plumula* – paddle cilia on the tip. **H** oral veil of *Berthella plumula* – cilia inside the lateral groove. **I** oral veil of *Berthella plumula* – paddle cilia on the outside, beneath the groove.

side the groove (Fig. 5A). In addition, clusters of paddle cilia could be detected in different parts of the groove (Fig. 5B). These paddle cilia are longer than the surrounding cilia without paddle-like ends. In the region of the mouth below the groove numerous paddle cilia are found (Fig. 5C). These paddle cilia could not be detected in the specimen that was fixed with the isoosmotic solution (method 2 / Fig. 5D). Moreover, no paddle cilia occur inside the groove of this specimen.

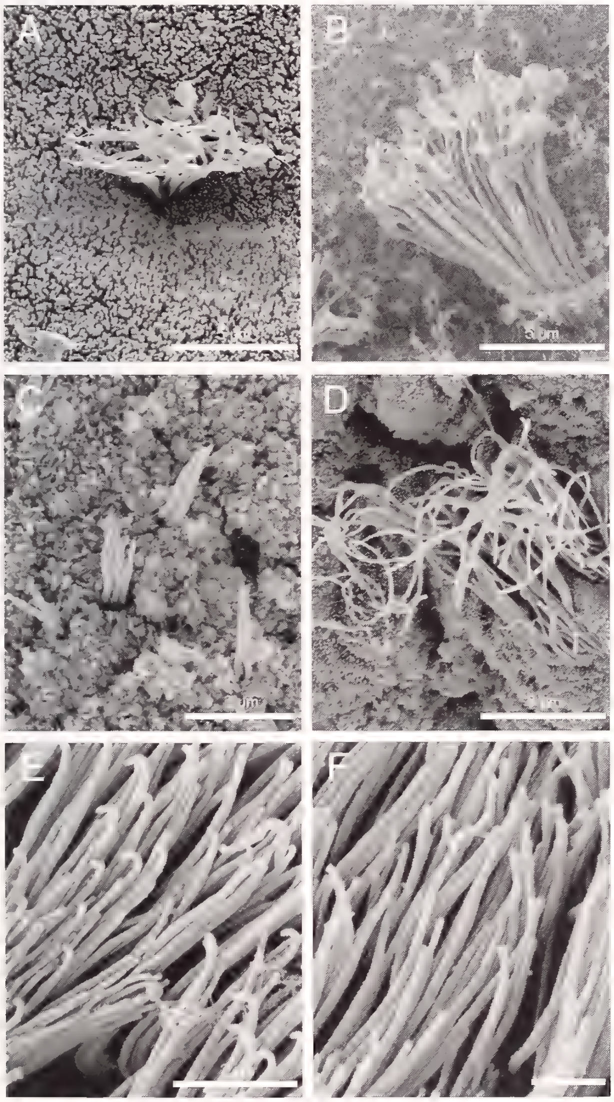

Fig. 4. Scanning electron microscopy of sensory regions of the CSOs of *Haminoea hydatis*. **A** lip organ fixed with method 1 – paddle cilia and cilia with straight tips in one tuft. **B** Hancock´s organ fixed with method 1 – tuft of paddle cilia. **C** lip organ fixed with method 2 – tuft of cilia with straight tips. **D** Hancock´s organ – tuft of cilia with straight tips. **E** head shield fixed with method 1 – cilia with curved tips. **F** head shield fixed with method 2 – cilia with straight tips.

The rhinophores and oral tentacles of *Aeolidiella glauca* are solid structures (Fig. 2A). Both were only fixed with method 1. Paddle-like structures could be detected on the tip of the rhinophores (Fig. 5E). Some of these paddle-like structures are not, as usually, found on the distal end of the cilia, but occur subapically. Paddle cilia are also present laterally on the oral tentacles (Fig. 5F). In addition, the cilia on the tip of the oral tentacles reveal swollen ends.

4. DISCUSSION

All investigated taxa and organs exhibit cilia with and without paddle-shaped ends. This fact might on the one hand support the assumption that paddle cilia are genuine structures. On the other hand it might be concluded that cilia with variable morphological features react differently to special fixation solutions.

The only specimen of *Aplysia punctata* exhibiting paddle cilia inside the groove of the rhinophore when fixed with method 1 was distinctly smaller than the other ones. This might possibly indicate that juveniles possess paddle cilia that get stretched during growth. It is also possible that this specimen was not handled with enough care which might be a reason for paddle cilia formation according to NIELSEN (1987). Thus the natural condition would be displayed by the straight tips. EHLERS & EHLERS (1978) also discovered that paddle cilia normally do not appear in the same quantity in all the individuals when several animals are fixed. Since paddle cilia are predominant inside the groove of the oral tentacle fixed with method 1, the cilia in this CSO seem to be more sensitive to paddle cilia formation than cilia in the rhinophore. The length of the cilia is equal in rhinophore and oral tentacle and cilia with straight tips are 4 µm longer than paddle cilia. This difference might be caused by rolling in of the tips of straight cilia resulting in paddle cilia formation. Thus paddle cilia would not be a genuine type of cilia but an artefact. The isoosmotic fixed specimens of both CSOs of *Aplysia punctata* reveal paddle cilia as well as cilia without paddle-like structures. This could indicate that paddle cilia are a distinct type of cilia. On the other side, it could also mean that SHORT & TAMM´S (1991) fixation method does not work as efficiently for opisthobranchs as it did for bivalves. The specimens could have also been exposed to another form of stress. Perhaps paddle cilia formation might even be induced by collecting or anaesthetisation of the animals. The findings for *Berthella plumula* are contrary to the results of SHORT & TAMM (1991), because isoosmotic fixation results in additional formation of paddle cilia, instead of decreasing the amount of these cilia. These results nevertheless reveal that cilia react differently to the application of variable fixation solutions, a fact

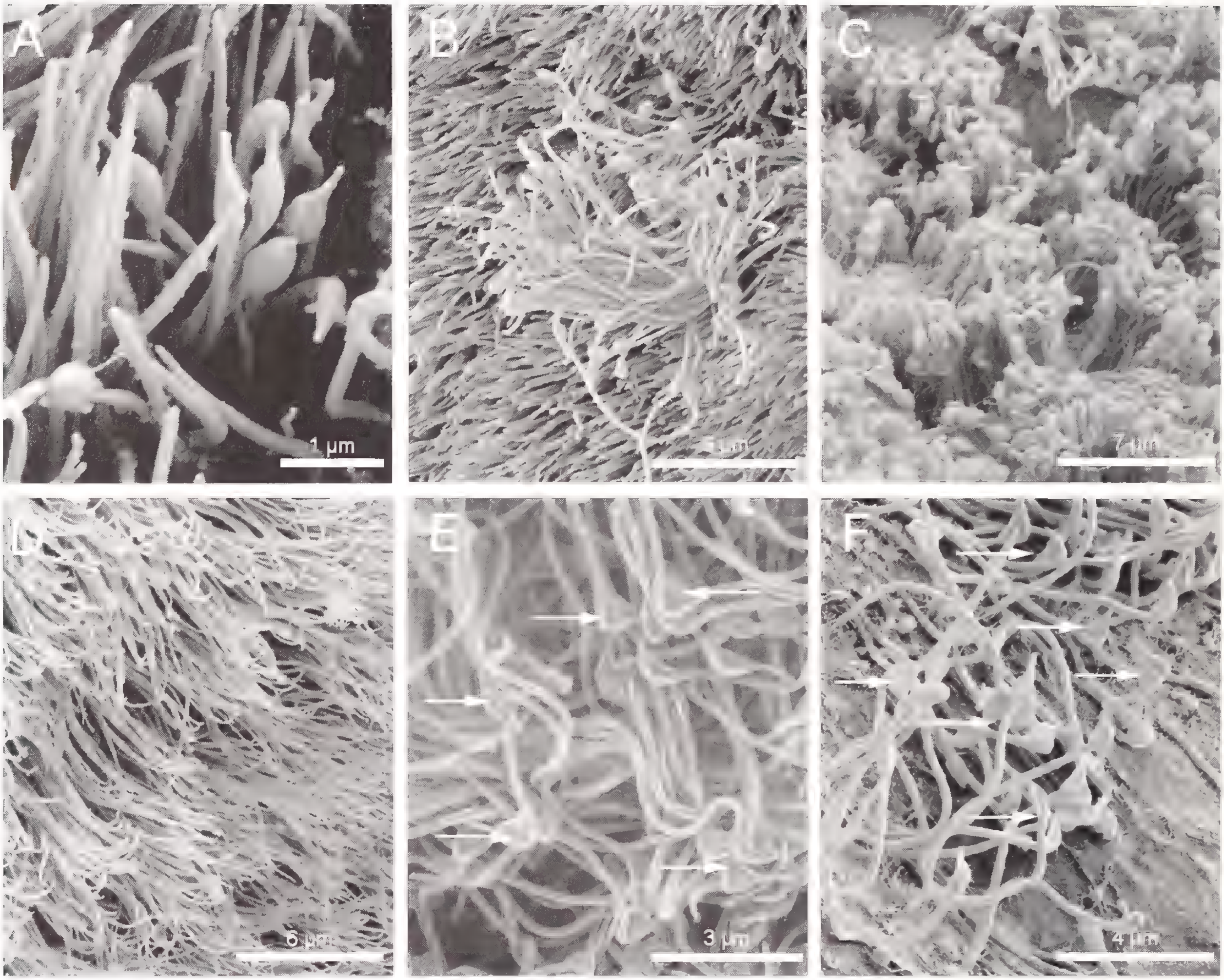

Fig. 5. Scanning electron microscopy of sensory regions of the CSOs of *Acteon tornatilis* and *Aeolidiella glauca* fixed with method 1 (except D). **A** *Acteon tornatilis* – cilia with dilated tips inside the groove. **B** *Acteon tornatilis* – tuft of paddle cilia inside the groove. **C** *Acteon tornatilis* – paddle cilia in the region of the mouth. **D** *Acteon tornatilis* – cilia in the region of the mouth. **E** rhinophore of *Aeolidiella glauca* – paddle cilia (arrows) on the tip. **F** oral tentacle of *Aeolidiella glauca* – paddle cilia (arrows) laterally.

that strengthens the assumption of paddle cilia being artefacts.

The tufts of paddle cilia found inside the groove of the head shield of *Acteon tornatilis* fixed with method 1 are longer than the surrounding cilia. BONE et al. (1982) investigated the nature of cilia in the endostyl of a tunicate. They argued that paddle cilia are artefacts and particularly prone to occur in long cilia. This seems to be true for *Acteon tornatilis*.

The lip and Hancock´s organ of *Haminoea hydatis* fixed with method 1 reveal cilia with and without paddle-like structures even in the same tuft. EHLERS & EHLERS (1978) described a similar situation for turbellarians. Not all the cilia of a given cell show paddle-like ends in these species, unmodified cilia also occur (EHLERS & EHLERS 1978). Morphological differences are apparently not the only reason for the formation of paddle cilia because it seems unlikely that cilia of one single tuft exhibit variable morphological features. Cilia with tips curved to the axonemes found on the hypoosmotically fixed head shield of *Haminoea hydatis* might be a developmental stage of paddle cilia since swelling of the ciliary membrane would lead to fully developed paddle cilia.

The fact that paddle cilia could not be detected on specimens of *Acteon tornatilis* and *Haminoea hydatis* fixed with method 2 corresponds to the findings of SHORT & TAMM (1991) and further indicates that paddle cilia are indeed artefacts.

The paddle-like structures found on the rhinophores and oral tentacles of *Aeolidiella glauca* fixed with method 1 are partly not located at the distal end of the cilia but are situated subapically. In addition numerous cilia with swollen ends were found on the oral tentacles. HEIMLER (1978) described these special forms as different types of paddle cilia. He distinguished three different types of paddle cilia. Type 1 has swollen, bulblike heads with a central straight axoneme. Type 2 paddle cilia are characterized by heads with a curved lateral axoneme and in type 3 paddle cilia the axoneme forms a loop. On the CSOs of *Aeolidiella glauca* type 1 and 2 paddle cilia could be detected whereas *Aplysia punctata* and *Berthella plumula* reveal type 3. Furthermore, HEIMLER (1978) supposed that these types represent different developmental stages of these cilia. Thus *Aeolidiella glauca* does not display the fully developed stage of paddle cilia.

MATERA & DAVIS (1982) investigated the distribution of paddle cilia on the opisthobranch *Pleurobranchaea californica*. Since paddle cilia only occurred in areas known to mediate chemoreception, they assumed them to be chemoreceptors. The current study shows that there are lots of other cilia with straight tips on the chemoreceptive structures of different Opisthobranchia, especially when using an isoosmotic fixation solution. This observation does not correspond to the conclusions of MATERA & DAVIS (1982), but indicates that paddle cilia might rather be artefacts.

EHLERS & EHLERS (1978) equally detected paddle-like structures only in sensory cells of the investigated Turbellaria. But they demonstrated that the number of paddles of sensory cilia increases in proportion to increasing osmolarity of the fixation solution and increasing temperature during fixation and concluded that paddle cilia are artefacts.

Altogether the current study enforces the assumption that paddle cilia are artefacts. Especially the results for *Acteon tornatilis* and *Haminoea hydatis* confirm that paddle cilia formation can be induced by the application of different fixation solutions. Nevertheless the results for *Aplysia punctata* and *Berthella plumula* leave the possibility that beyond being artefacts paddle cilia might occur naturally in a lesser amount. This speculation needs to be proven in living, unstressed animals.

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Preliminary study on molecular phylogeny of Sacoglossa and a compilation of their food organisms*

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Abstract. The first molecular analysis of the Sacoglossa based on the 16Sr DNA gene (partial), with 39 species and 59 specimens analysed, is presented. A saturation of substitution is observed, as well as conflict in the data concerning certain taxa. Therefore the phylogenetic relationship presented here has to be considered as preliminary. Many results are congruent with the analysis of JENSEN (1996) based on morphological characters. Plakobranchacea are monophyletic. *Elysiella pusilla* is nested within the genus *Elysia* and therefore synonymy of *Elysiella* with *Elysia* confirmed. The position of *Plakobranchus* remains unclear, but a closer affinity to *Elysia* than to *Thuridilla* seems most likely. Major differences lie in the paraphyly of the Oxynoacea, but only few members of this taxon have been included. A compilation of available data on food algae is presented and the data are discussed under the light of the phylogenetic relationship presented here.

Keywords. Opisthobranchia, molecular systematics, SplitsTree, Chlorophyta, evolution, 16S rDNA.

1. INTRODUCTION

Sacoglossa is a small group of Opisthobranchia with about 250 to 300 described species (JENSEN 1997a). Animals are small and species larger than 30 mm are rare. The monophyly of this group is well supported (JENSEN 1996) although their phylogenetic position relating to other groups of Opisthobranchia is unresolved (DAYRAT et al. 2001; DAYRAT & TILLIER 2002; GRANDE et al. 2004; VONNEMANN et al. 2005; WÄGELE & KLUSSMANN-KOLB 2005).

The first and only phylogeny of Sacoglossa based on morphological data was presented by JENSEN (1996) applying Hennigian principles. Her analysis was performed on genus level, except for the genus *Elysia* with four included species. One of her results was a differentiation into two major clades, the shelled Oxynoacea and the shell-less Plakobranchacea. The latter comprise the monophyletic Plakobranchoidea and the monophyletic Limapontioidea. *Cylindrobulla* appeared as the most basal taxon within her analysis. GOSLINER (1995) performed a morphologically based analysis concentrating on the genus *Thuridilla*. An analysis of the family Plakobranchidae based on a genetic marker (COI) was published lately (BASS & KARL 2006). No further phylogenetic analyses have been performed up to now.

Sacoglossa is feeding nearly exclusively on siphonalean or siphonocladalean Chlorophyta. They penetrate the cell wall with their uniseriate radula and suck out the cell sap. Noteworthy is the possibility of several sacoglossans to incorporate the chloroplasts from their food intracellular in their digestive gland and partially perform photosynthesis. This was first recorded by KAWAGUTI & YAMASU (1965) and most recently analysed by EVERTSEN et al. (2007) (for a review see RUMPHO et al. 2000). For several sacoglossans reception of polysaccharides and amino acides from these chloroplasts is documented (TRENCH 1973; WILLIAMS & WALKER 1999 after Greene & Muscatine 1972). In addition, many members of the Sacoglossa are able to incorporate secondary metabolites from their food and use these as a chemical defense (CIMINO & GHISELIN 1998; CIMINO et al. 1999; GAVAGNIN & FONTANA 2000; MARÍN & ROS 2004; CIMINO & GAVAGNIN 2006).

JENSEN (1997a: 313) was the first who discussed a possible correlation between the evolution of morphological characters of the Sacoglossa and the possible evolution of the food plants. She argued that more investigations are needed: “Rigorous application of cladistic methodology in coevolution analysis requires fully resolved phylogenies of the `hosts` as well as the `associates`.” Intention of this study was to fill this gap by analysing the phylogeny of Sacoglossa with molecular data and by including many more species. New available data on food organisms in Sacoglossa are presented, which might help to elaborate co-evolutionary processes.

2. MATERIALS AND METHODS

2.1. Biological material

58 specimens including 38 species of sacoglossans were used for the phylogenetic reconstruction. Locality, date of collection and accession numbers are indicated in Table 1. According to the results of JENSEN (1996) and unpublished data of the senior author, *Cylindrobulla beauii* (Cylindrobullidae, Opisthobranchia) was chosen as outgroup species. *Cylindrobulla* and Sacoglossa share synapomorphies (presence of a shell, adductor muscle, and a lamellate gill (JENSEN 1996)), but also lack synapomorphies of the Sacoglossa (e.g. ascus), and show plesiomorphic characters (e.g. triangular shaped teeth, large shell).

2.2. DNA extraction, amplification and sequencing

DNA was extracted from alcohol-preserved specimens by means of NucleoSpin® Tissue-Kit by Machery-Nagel or Dneasy® Blood and Tissue Kit by Quiagen, guided by the enclosed protocol. A segment of the 16Sr DNA gene was amplified with primer pairs, LR-J-12887 5'-GGA GCT CCG GTT TGA ACT CAG ATC-3' and LR-N-13398 5'-CGG CCG CCT GTT TAT CAA AAA CAT-3'. Amplification reactions (50µl) consisted of 39.15µl ddH$_2$O, 5µl 10X PCR Buffer without MgCl$_2$ (Fermentas), 4µl MgCl$_2$ (25mM), 0.15µl Taq-Polymerase (5U/µl), 0.4µl of each Primer (10pmol/µl) and 0.5µl DNA. The PCR was carried out in the Gene Amp PCR System 9600 by Perkin Elmer® under following conditions: 95°C for 240s, followed by 9 Touch-down-cylces of 45s at 94°C, 45s at 56(-1)°C, 90s at 72°C, followed by 25 amplification-cycles of 45s at 94°C, 45s at 48°C, 90s at 72°C and a final extension at 72°C for 10min followed by cooling down to 4°C. Amplicons were purified by means of NucleoSpin® Extrat II by Machery-Nagel, guided by the enclosed protocol. The mass of the amplicons was estimated by comparing ethidium bromide staining intensity of 5µl of each purified reaction.

Cycle sequencing reactions (Cycle Sequencing Kit BigDye® Terminator v1.1 by Applied Biosystems) were carried out in the Gene Amp PCR System 9600 by Perkin Elmer® under following conditions: 96°C for 120s followed by 15 cycles of 10s at 96°C, 5s at 50°C, 150s at 60°C followed by cooling down to 4°C. Reaction products were purified by adding 40µl water containing Dextranblau, 5µl natriumacetate (3M, pH4.6) and 125µl pure ethanol, centrifuging for 15min, taking supernatant, adding 500µl fresh 70% ethanol, centrifuging for 5min, taking supernatant, and were dried at 37°C for 30-40min. The fluorescently labeled products were size sorted and visualized using an ABI PrismTM 377 DNA Sequencer by Applied Biosystems. The sequences were extracted with Sequencing Analysis 3.0. The sequences of the reverse primer were complemented with Factura 2.0.1 and sequences of both strands were compared and synchronised with Sequence Navigator.

The gene fragments were aligned by applying Muscle3.7 (EDGAR 2004a; EDGAR 2004b) and the resulting alignment was verified by eye. Length of the alignment was 478 base pairs.

2.3 Phylogentic reconstruction

A Bayesian analysis was performed with MrBayes 3.1.2 (HUELSENBECK & RONQUIST 2001; HUELSENBECK & BOLLBACK 2001). Maximum Parsimony analysis, Neighbor-joining analysis and Maximum likelihood analysis have been performed with PAUP* 4.0b10. Modeltest 3.7 (POSADA & BUCKLEY 2004) selected as best-fit model the GTR+G+I-model (AIC). Therefore, neighbour-joining analysis was conducted on a GTR-model and Maximum Likelihood analysis and Bayesian analysis on a GTR+G+I-model. Saturation of substitutions was tested against patristic distances as well as against distances obtained with the GTR-model. A posteriori statistical analysis could not be performed due to long calculation time of bootstrapping methods. For visualizing conflict in the data set, which seemed obvious after the analyses, SplitsTree4 (HUSON & BRYANT 2006) was applied. A Neighbour-Net analysis was performed applying the K2P-model.

3. RESULTS

Saturation in substitutions of the partial 16Sr DNA obtained by using the GTR model is shown in Figure 1. The graph approaches a plateau indicating a saturation of substitutions. When splitting the data set into subgroups (family or genera), saturation was less evident for most groups, but not e.g. the genus *Elysia* or *Thuridilla*. Substitution rates were also less saturated, when using p-distances (not shown here).

3.1. Phylogenetic reconstruction

A maximum parsimony analysis produced 81 shortest topologies with a length of 1401 steps. The 50%-Majority-Rule tree is shown in Figure 2. Within the monophyletic Plakobranchacea, the family Polybranchiidae and the polybranchiid genus *Cyerce* are also monophyletic. The monophyletic genus *Ercolania* appears as the sistertaxon to the Polybranchiidae. The families Plakobranchidae and Limapontiidae are not monophyletic, the genera *Elysia* and *Thuridilla* are also paraphyletic. *Plakobranchus* groups as sistertaxon of several *Elysia* species. The shelled Oxynoacea are basal. They are paraphyletic as well as the family Juliidae and Oxynoidae. The position of *Oxynoe viridis* is unresolved.

In the Neighbor-joining analysis (not presented here), Plakobranchacea are monophyletic, as well as the family Polybranchiidae and the genus *Thuridilla*. *Bosellia mimetica* (Boselliidae) groups in the family Plakobranchidae, rendering this family paraphyletic. Limapontiidae is paraphyletic again, since *Ercolania* and *Stiliger* do not group together. The genus *Elysia* again comprises *Elysiella* and *Plakobranchus* and is polyphyletic in this analysis. *Plakobranchus* is sistertaxon to the same *Elysia*-complex as in the maximum parsiomony analysis. Similar to the maximum parsimony analysis, *Elysia benettae* is the sistertaxon to *Elysiella pusilla*. Monophyletic *Ercolania* appears as the most basal genus of the Plakobranchacea. Oxynoacea are basal and paraphyletic. The families Juliidae and Oxynoidae again are not monophyletic. Similar as in the MP analysis, *Tamanovalva* is the sistertaxon to the Plakobranchacea. The position of *Oxynoe viridis* is unclear.

Two identical trees were found in the Maximum-likelihood analysis; the resulting tree is shown in Figure 3. Plakobranchacea is monophyletic, as well as the families Plakobranchidae and Polybranchiidae. Boselliidae is sistertaxon to the Plakobranchidae. The genus *Thuridilla* is monophyletic. *Elysiella pusilla* with *Elysia benettae* as sistertaxon groups in the genus *Elysia*, rendering this genus paraphyletic. In this analysis *Plakobranchus ocellatus* is the sistertaxon to all *Elysia*-species (including *Elysiella*) and monophyletic *Thuridilla* to this *Plakobranchus/Elysia* clade. Limapontiidae again is paraphyletic. Contrary to the other analyses, *Ercolania* is not monophyletic. The two species represent the most basal Plakobranchacea. The Oxynoacea and Oxynoidae are paraphyletic again, but contrary to all other analyses, the Juliidae with the genera *Julia* and *Tamanovalva* represent a monophyletic group. The position of *Oxynoe viridis* is unresolved.

The cladogram based on the analysis with MrBayes is shown in Figure 4. Plakobranchacea is monophyletic, but resolution within that taxon is low. *Elysia* (without *E. benettae*), *Elysiella/Elysia bennettae* complex and *Plakobranchus* form a monophyletic clade, but their position is

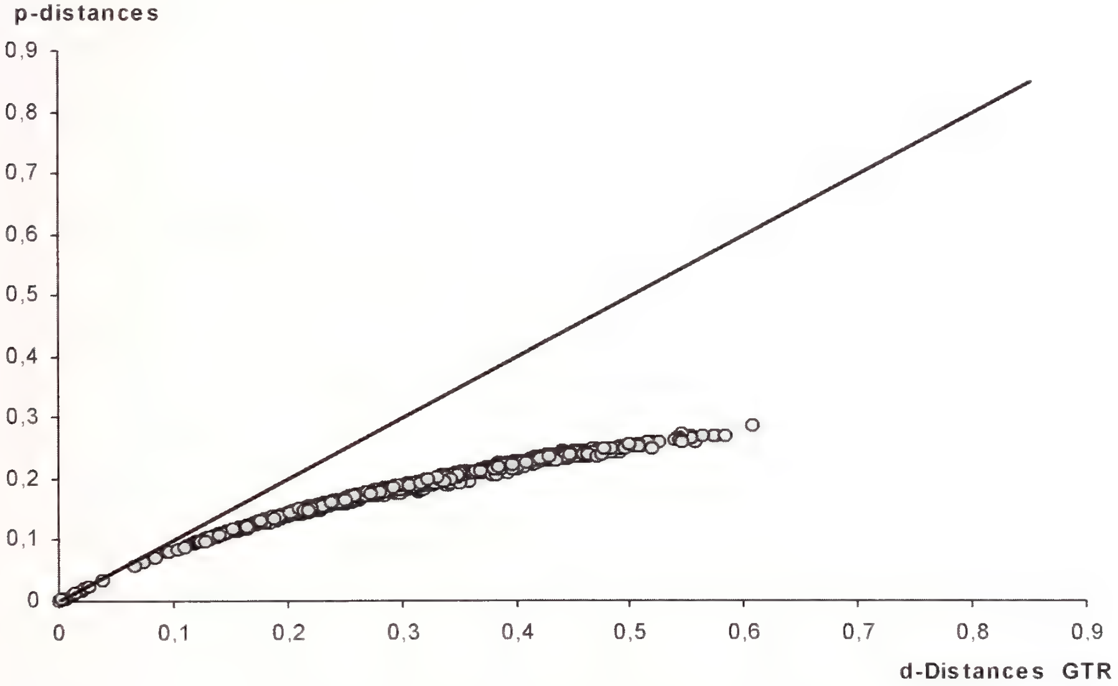

Fig. 1. Saturation of substitution of the 16Sr DNA gene (partial) used in this analysis. The straight line is the bisector. Distances are calculated as patristic distances (y-axis) against d-distances calculated by applying the GTR model (x-axis).

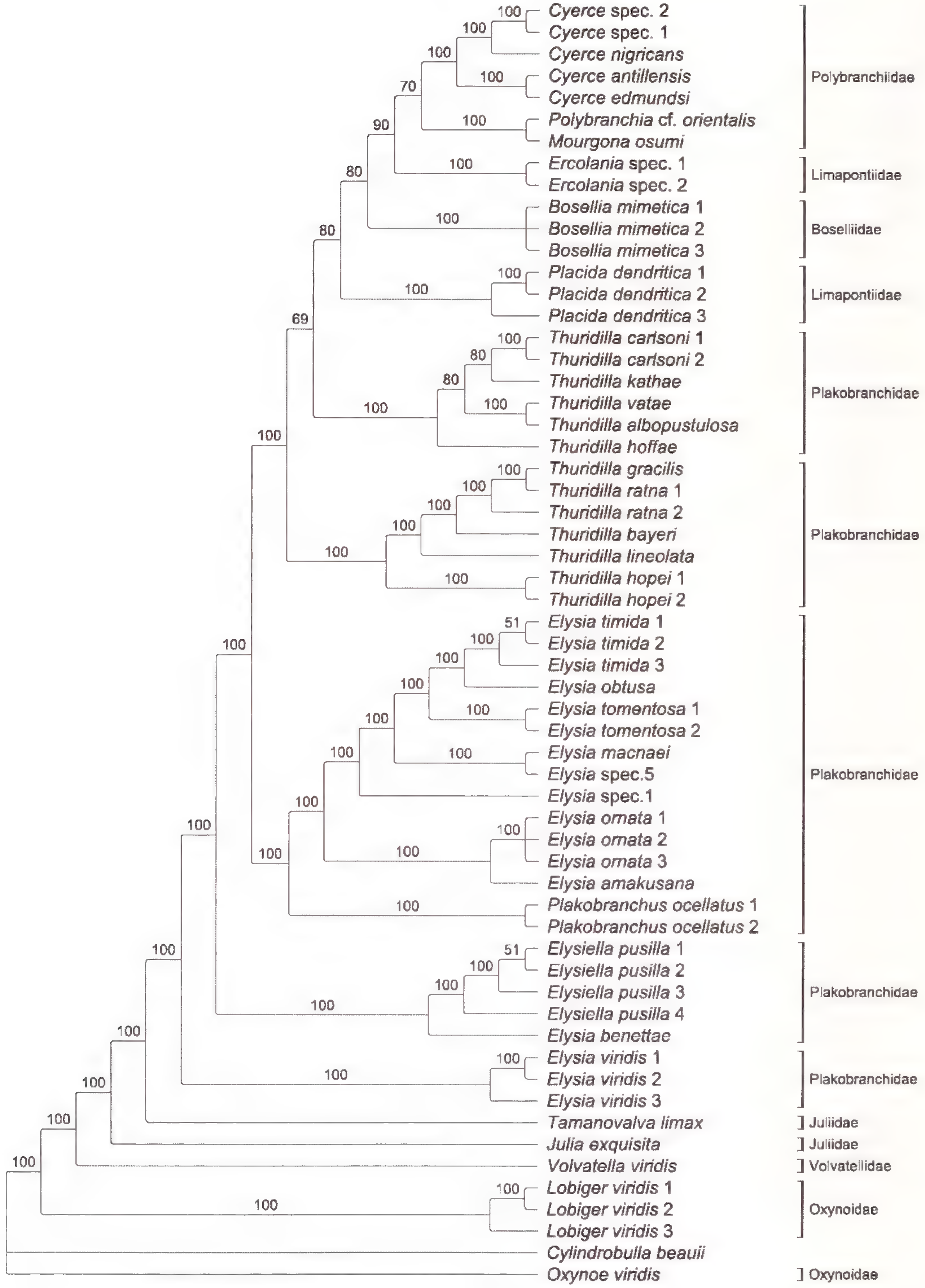
Cyerce spec. 2
Cyerce spec. 1
Cyerce nigricans
Cyerce antillensis
Cyerce edmundsi
Polybranchia cf. orientalis
Mourgona osumi
Ercolania spec. 1
Ercolania spec. 2
Bosellia mimetica 1
Bosellia mimetica 2
Bosellia mimetica 3
Placida dendritica 1
Placida dendritica 2
Placida dendritica 3
Thuridilla carlsoni 1
Thuridilla carlsoni 2
Thuridilla kathae
Thuridilla vatae
Thuridilla albopustulosa
Thuridilla hoffae
Thuridilla gracilis
Thuridilla ratna 1
Thuridilla ratna 2
Thuridilla bayeri
Thuridilla lineolata
Thuridilla hopei 1
Thuridilla hopei 2
Elysia timida 1
Elysia timida 2
Elysia timida 3
Elysia obtusa
Elysia tomentosa 1
Elysia tomentosa 2
Elysia macnaei
Elysia spec.5
Elysia spec.1
Elysia ornata 1
Elysia ornata 2
Elysia ornata 3
Elysia amakusana
Plakobranchus ocellatus 1
Plakobranchus ocellatus 2
Elysiella pusilla 1
Elysiella pusilla 2
Elysiella pusilla 3
Elysiella pusilla 4
Elysia benettae
Elysia viridis 1
Elysia viridis 2
Elysia viridis 3
Tamanovalva limax
Julia exquisita
Volvatella viridis
Lobiger viridis 1
Lobiger viridis 2
Lobiger viridis 3
Cylindrobulla beauii
Oxynoe viridis
Polybranchiidae
Limapontiidae
Boselliidae
Limapontiidae
Plakobranchidae
Plakobranchidae
Plakobranchidae
Plakobranchidae
Plakobranchidae
Juliidae
Juliidae
Volvatellidae
Oxynoidae
Oxynoidae
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Fig. 2. Sacoglossa; 16Sr DNA gene: Maximum Parsimony analysis, 50% Majority Rule consensus tree.

unresolved. This complex and two *Thuridilla* complexes (representing all Plakobranchidae) and *Bosellia* form the next higher unresolved monophyletic clade.

Polybranchiidae and within that family the genus *Cyerce*, is monophyletic. The family Limapontiidae and the limapontiid genus *Ercolania* are paraphyletic. The Oxynoacea and Oxynoidae are paraphyletic. The Juliidae are not resolved and the position of *Oxynoe viridis* remains again unclear.

The analysis of the dataset with SplitsTree visualises the incongruencies in the dataset and the resulting incongruencies in the different cladograms. Figure 5 shows a network connecting all terminal taxa. Parallel edges of same length within the network visualise a split between two groups. Members of each group share same characters (assumed apomorphic nucleotides for that group). Fit value of the analysis is 95.06, indicating that actually all conflicts are visualised in the figure. No long branch taxa can be identified. Very well supported is the split between Oxynoacea + *Cylindrobulla* and Plakobranchacea, indicated by the long edges. Also well supported are splits between species (e.g. *Placida dendritica*, *Elysia timida* or *Elysia viridis*) and the rest of the sequences. No split between outgroup taxon *Cylindrobulla* and Sacoglossa exists (Fig. 5 and Fig. 6, the latter showing the analysis with a reduced data set for better visualisation). But a split between *Cylindrobulla* + *Tamanovalva limax* + *Oxynoe viridis* against all other sequences can be observed (Fig. 5). Phylogenetic signal (shown as splits) is already low on genus level (e.g. *Ercolania*), or not existing (e.g. *Cyerce, Elysia* or *Thuridilla)*. A separate analysis of all *Thuridilla* species (Fig. 7) shows the close affinities of *T. ratna* and *T. gracilis*, whereas *T. bayeri* appears separate.

3.3. Food spectrum in Sacoglossa

A compilation of available data on food organisms of sacoglossans is presented in Table 2. Food organisms of *Cylindrobulla* are not known. All members of Oxynoacae feed on species of *Caulerpa*. In contrast, species of the Plakobranchacea have a much wider food spectrum:

Members of the family Boselliidae seem to be restricted to the order Caulerpales (Bryopsidophyceae), mainly feeding on *Halimeda*. Within Plakobranchidae, *Elysia* shows the widest range on food organisms, containing Heterokontophyta (*Vaucheria, Padina, Biddulphia*) and angiospermes (seagrasses). *Elysia timida* and *Elysia filicauda* feed on *Acetabularia* (Dasycladales). KREMER and JANKE (1988) claimed that chloroplasts of the algal genus *Codium* have been found in *Elysia timida* as well. Only for one species of *Thuridilla*, *T. hopei*, data are available: *Derbesia* and *Cladophora*. The only two references for *Plakobranchus ocellatus* are based on observations in the laboratory (JENSEN 1980a after Switzer-Dunlap 1975; HIROSE 2005 after Adachi 1991). This species feeds on *Chlorodesmis* and *Udotea*. Interesting is the food organism of *Pattyclaya*, which, according to JENSEN (1992), is *Caulerpa*.

Polybranchiidae feed on species of the orders Bryopsidales and Caulerpales (Bryopsidophyceae) except for *Mourgona* (*Cymopolia* (JENSEN 1981; CLARK 1994) and *Acetabularia* (HAMATANI 1994), Dasycladales, Dasycladophyceae). Hermaeidae also exhibit a broader spectrum of food organisms: The genus *Hermaea* is characterized by feeding on Rhodophyta (GRAHAM 1955 after Pelseneer 1935; TAYLOR 1968; TAYLOR 1971; KREMER & SCHMITZ 1976; KREMER & SCHMITZ 1976 after Cornet & Marche-Marchad 1951; JENSEN& CLARK 1983; JENSEN 1993a, b; WILLIAMS & WALKER 1999 after JENSEN 1983) except *Hermaea vancouverensis* consuming *Isthmia nervosa*, a diatom (WILLIAMS & GOSLINER 1973). *Aplysiopsis* feeds on algae belonging to the orders Cladophorales (JENSEN 1980a after Gonor 1961; JENSEN 1980a after Greene 1970; JENSEN 1993a; TROWBRIDGE 1993; JENSEN 1995; WILLIAMS & WALKER 1999 after Jensen 1983) or Ulvales (JENSEN 1980a after Gonor 1961; JENSEN 1980a after Greene 1970; TROWBRIDGE 1993), *Costasiella* feeds on algae belonging to the orders Bryopsidales (CLARK & BUSACCA 1978; JENSEN 1980a, 1981; CLARK et al. 1981; CLARK 1984; JENSEN 1993a; CLARK 1994; WILLIAMS & WALKER 1999 after Jensen 1980, 1981, 1983) and Caulerpales (JENSEN 1981; WILLIAMS & WALKER 1999 after Jensen 1980, 1981, 1983) (Bryopsidophyceae), Cladophorales (WILLIAMS & WALKER 1999 after Jensen 1980, 1981, 1983) and *Vaucheria* (Heterokontophyta) (JENSEN 1990a, b). Limapontiidae show the most extraordinary food range. Species of the genus *Limapontia* feed on Cladophorales (GRAHAM 1955 after Gascoigne 1952; JENSEN 1975, 1980a after Gascoigne 1956), but also Bryopsidales (JENSEN 1975, 1980a after Gascoigne 1956), Ulvales (GRAHAM 1955 after Gascoigne 1952) and the heterokontophyte *Vaucheria* (GRAHAM 1955 after Gascoigne 1954; GASCOIGNE & SARTORY 1974; JENSEN 1980a after Gascoigne 1956; HARTOG 1959). *Alderia* also feeds on *Vaucheria* (EVANS 1953; GRAHAM 1955 after Gascoigne 1954; CLARK 1975; JENSEN 1980a after Hartog 1959; KRUG & MANZI 1999), but there is one reference for the cladophoralean *Rhizoclonium* (GRAHAM 1955 after Gascoigne 1954). The genus *Placida* mainly feeds on species of Bryopsidales (BRÜEL 1904; GRAHAM 1955 after Gascoigne 1954; BLEAKNEY 1989 after Thompson 1976 and after Millen 1980; JENSEN 1980a; JENSEN 1980a after Monselise & Mienis 1977 and after Schmekel 1982, JENSEN 1981, 1990b; MARZO, DI et al. 1993; TROWBRIDGE 2004 after Willan & Morton 1984, after Burn 1989 and after Trowbridge 1998b) and *Codium* (Brüel 1904 after Hecht 1895; Graham 1955 after Gascoigne 1954; Clark 1975; Trowbridge 2004 after Willan & Morton 1984, after Burn 1989 and after Trowbridge 1998b; Behrens 2004) (Bryopsidophyceae). Brüel (1904) referenced to Trinchese 1876 that *Placida dendritica* feeds on *Ulva* doubting this fact at the same time. The observation that *Placida dendritica* ate another sacoglossa (Marcus du Bois-Reymond 1972) seems to be a particular case. *Placida kingstoni* extended its diet to *Cladophora* (Jensen 1981). The genus *Ercolania* prefers Cladophorales (Clark 1975; Jensen 1980a; Jensen 1980a after Trinchese 1872, after Rao 1937, after Schmekel 1968, after Rasmussen 1973 and after Usuki 1977; Jensen 1981; Marín & Ros 1992 after Marín & Ros 1988; Jensen 1993a; Marzo, di et al. 1993; Clark 1994; Jensen 1999; Grzymbowski et al. 2007), one reference for *Caulerpa* (Jensen 1980a after Edmunds 1963) is not confirmed again. *Stiliger fuscovittatus* feeds on red algae (Jensen 1980a after Lance 1962). Unusual feeding strategies in the family show *Calliopea oophaga, Olea hansineensis* and *Stiliger vesiculosus*, they consume eggs of other Opisthobranchia (Jensen 1986; Lemche 1974; Crane 1971; Jensen 1999 after Haefelfinger 1962).

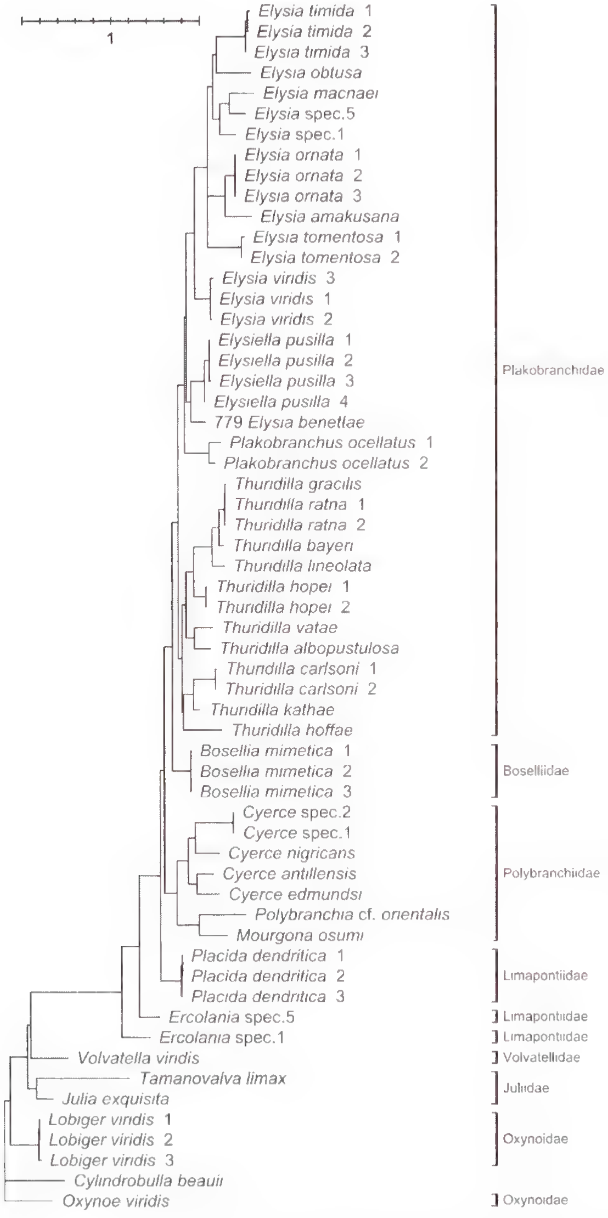

1
Elysia timida 1
Elysia timida 2
Elysia timida 3
Elysia obtusa
Elysia macnaei
Elysia spec.5
Elysia spec.1
Elysia ornata 1
Elysia ornata 2
Elysia ornata 3
Elysia amakusana
Elysia tomentosa 1
Elysia tomentosa 2
Elysia viridis 3
Elysia viridis 1
Elysia viridis 2
Elysiella pusilla 1
Elysiella pusilla 2
Elysiella pusilla 3
Elysiella pusilla 4
779 Elysia benettae
Plakobranchus ocellatus 1
Plakobranchus ocellatus 2
Thuridilla gracilis
Thuridilla ratna 1
Thuridilla ratna 2
Thuridilla bayeri
Thuridilla lineolata
Thuridilla hopei 1
Thuridilla hopei 2
Thuridilla vatae
Thuridilla albopustulosa
Thuridilla carlsoni 1
Thuridilla carlsoni 2
Thuridilla kathae
Thuridilla hoffae
Bosellia mimetica 1
Bosellia mimetica 2
Bosellia mimetica 3
Cyerce spec.2
Cyerce spec.1
Cyerce nigricans
Cyerce antillensis
Cyerce edmundsi
Polybranchia cf. orientalis
Mourgona osumi
Placida dendritica 1
Placida dendritica 2
Placida dendritica 3
Ercolania spec.5
Ercolania spec.1
Volvatella viridis
Tamanovalva limax
Julia exquisita
Lobiger viridis 1
Lobiger viridis 2
Lobiger viridis 3
Cylindrobulla beauii
Oxynoe viridis
Plakobranchidae
Boselliidae
Polybranchiidae
Limapontiidae
Limapontiidae
Limapontiidae
Volvatellidae
Juliidae
Oxynoidae
Oxynoidae

Fig. 3. Sacoglossa; 16Sr DNA gene: Maximum Likelihood tree (GTR+G+I-model, AIC).

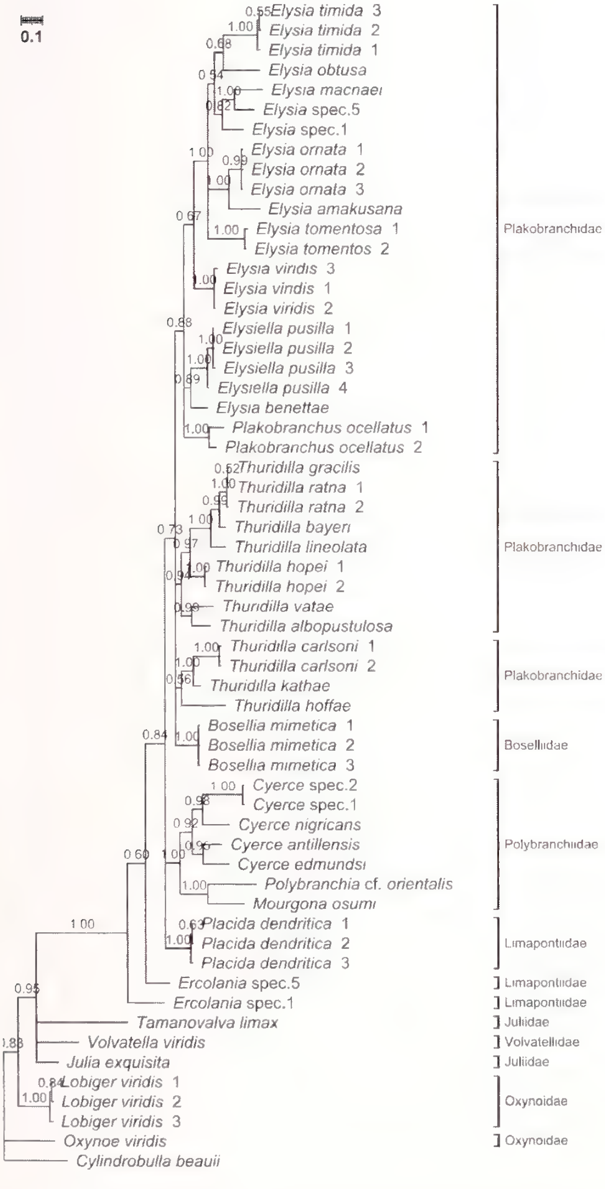
In Figure 8, the available data of higher food taxa are mapped onto the cladogram of the Maximum Likelihood analysis. Two references are not included: Kremer and Janke (1988) determined chloroplasts in *Elysia timida* as chloroplasts of *Codium* neither describing the origin of the included REM-slide nor giving a reference. *Elysia timida* was never described feeding on *Codium*, a misdetermination of the chloroplasts is therefore likely. Brüel (1904) already doubted Trinchese's information that *Placida dendritica* feeds on *Ulva*. Trinchese's observation was never confirmed over the following years.

4. DISCUSSION

4.1. Phylogeny of Sacoglossa

The Oxynoacea, comprising the shelled sacoglossans, are paraphyletic in all phylogenetic analyses. Applying SplitsTree, there exists no information for a split *Cylindrobulla* against Sacoglossa. But according to the very long edges, there is much information for a split *Cylindrobulla* + Oxynoacea against Plakobranchacea. Jensen (1996) mentioned an eversible oral tube, a long, rod-shaped preradular tooth and a large female genital papilla as synapomorphies for the Oxynoacea. These characters are not present in *Cylindrobulla*. Using a cephalaspid as outgroup and including *Cylindrobulla* as part of the ingroup is not applicable for this gene, since it shows already a high substitution rate for the present data set. But the position of *Cylindrobulla* as member of the Oxynoacea has to be reconsidered by using a more conservative gene, as 16S has proven to be. CO1 is also not apt for this investigation, since it shows high substitution rates on nucleotide level and is not informative on amino acid level (unpublished data of the authors). The unresolved position of *Oxynoe viridis* at the base of the cladograms is peculiar. The genus never groups with *Lobiger*, both usually united under the Oxynoidae. A contamination is unlikely due to high affinity with opisthobranch sequences. SplitsTree visualizes uniting positions with *Cylindrobul-*

la and *Tamanovalva limax*, which might present homoplastic characters. The Juliidae are monophyletic only in the Maximum Likelihood analysis, but support is present in the SplitsTree analysis. According to JENSEN (1996) the bivalved shell and small, paired pharyngeal pouches are autapomorphies of this family. It is most unlikely that the bivalved shell has evolved several times independently, as several phylogenetic analyses presented here would suggest.


0.1
Elysia timida 3
Elysia timida 2
Elysia timida 1
Elysia obtusa
Elysia macnaei
Elysia spec.5
Elysia spec.1
Elysia ornata 1
Elysia ornata 2
Elysia ornata 3
Elysia amakusana
Elysia tomentosa 1
Elysia tomentos 2
Elysia viridis 3
Elysia viridis 1
Elysia viridis 2
Elysiella pusilla 1
Elysiella pusilla 2
Elysiella pusilla 3
Elysiella pusilla 4
Elysia benettae
Plakobranchus ocellatus 1
Plakobranchus ocellatus 2
Thuridilla gracilis
Thuridilla ratna 1
Thuridilla ratna 2
Thuridilla bayeri
Thuridilla lineolata
Thuridilla hopei 1
Thuridilla hopei 2
Thuridilla vatae
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Cyerce spec.1
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Cyerce antillensis
Cyerce edmundsi
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Placida dendritica 2
Placida dendritica 3
Ercolania spec.5
Ercolania spec.1
Tamanovalva limax
Volvatella viridis
Julia exquisita
Lobiger viridis 1
Lobiger viridis 2
Lobiger viridis 3
Oxynoe viridis
Cylindrobulla beauii
Plakobranchidae
Plakobranchidae
Plakobranchidae
Boselliidae
Polybranchiidae
Limapontiidae
Limapontiidae
Limapontiidae
Juliidae
Volvatellidae
Juliidae
Oxynoidae
Oxynoidae

Fig. 4. Sacoglossa; 16Sr DNA gene: Bayesian Analysis, 50%-Majority Rule consensus tree with posterior probabilities (GTR+G+I-model, AIC).

In all analyses, the Plakobranchacea sensu JENSEN (1996) are monophyletic and this is visualized very well by the long edges separating this taxon from Oxynoacea + *Cylindrobulla*. But this is not the case for the higher ranking taxa Plakobranchoidea and Limapontioidea. Whereas the former taxon was recognized at least in the maximum likelihood and MrBayes analyses, the Limapontioidea with the genera *Placida* and *Ercolania* (both members of the Limapontiidae) never appeared monophyletic. This is of special interest taking into consideration the ongoing discussion on the validity of *Placida*, *Ercolania* and *Stiliger* as three separate genera (e.g. MARCUS DU BOIS-REYMOND 1982; JENSEN 1985). In JENSEN's (1996) analysis, the Limapontiidae and the genus *Costasiella* (Costasiellidae) form a partly unresolved group. Limapontiidae is characterized by two visceral ganglia instead of three or more (JENSEN 1996).

Contrary to Jensen's analysis, the Polybranchiidae form a monophyletic group with exactly the same branching pattern of the six species (three genera) in all analyses, although no support can be seen in the splits graph. Interesting is the sister taxa relationship of the two Atlantic *Cyerce* species, *C. antillensis* and *C. edmundsi*. MARCUS DU BOIS-REYMOND (1982) and HAMATANI (1994) considered *Cyerce edmundsi* Thompson, 1977 as synonymous with *Mourgona germaineae* Marcus & Marcus, 1970. Assignment of *Cyerce edmundsi,* as described by THOMPSON (1977), to the genus *Cyerce* contradicts diagnostic features of this genus: „The cerata proved to contain abundant lobules of the digestive gland“ (THOMPSON 1977: 137). *Cyerce* is seperated from the other Polybranchiidae by having no branches of the digestive gland in the cerata (MARCUS DU BOIS-REYMOND 1982 after Eliot 1910). According to the results of this study, *Cyerce edmundsi* is related to *Cyerce* and not *Mourgona*. A re-arrangement of the genera and species is too early, more taxa of Limapontioidea with the families Polybranchiidae, Hermaeidae, Costasiellidae, and Limapontiidae have to be added in future investigations to clarify validity of these taxa.

Within the usually monophyletic Plakobranchoidea, two families have been considered, the monogeneric Boselliidae and the species rich family Plakobranchidae. The genus *Bosellia* comprising only five species (JENSEN 1997a) was always a taxon to debate. PRUVOT-FOL (1954) settled *Bosellia* within the family Polybranchiidae. She interpreted the dorsal apertures on the surface as a reminiscence of lost cerata: „Des «orifices» semés sur la partie dorsale font penser que l`animal décrit est incomplet, c`est-à-dire qu`il a perdu ses papilles.“ (PRUVOT-FOL 1954: 180). However, PRUVOT-FOL has not examined a specimen of *Bosellia* by herself but followed the first description of TRINCHESE written in 1891. PORTMANN (1958) re-described the species and denied the existence of pores on the dor-

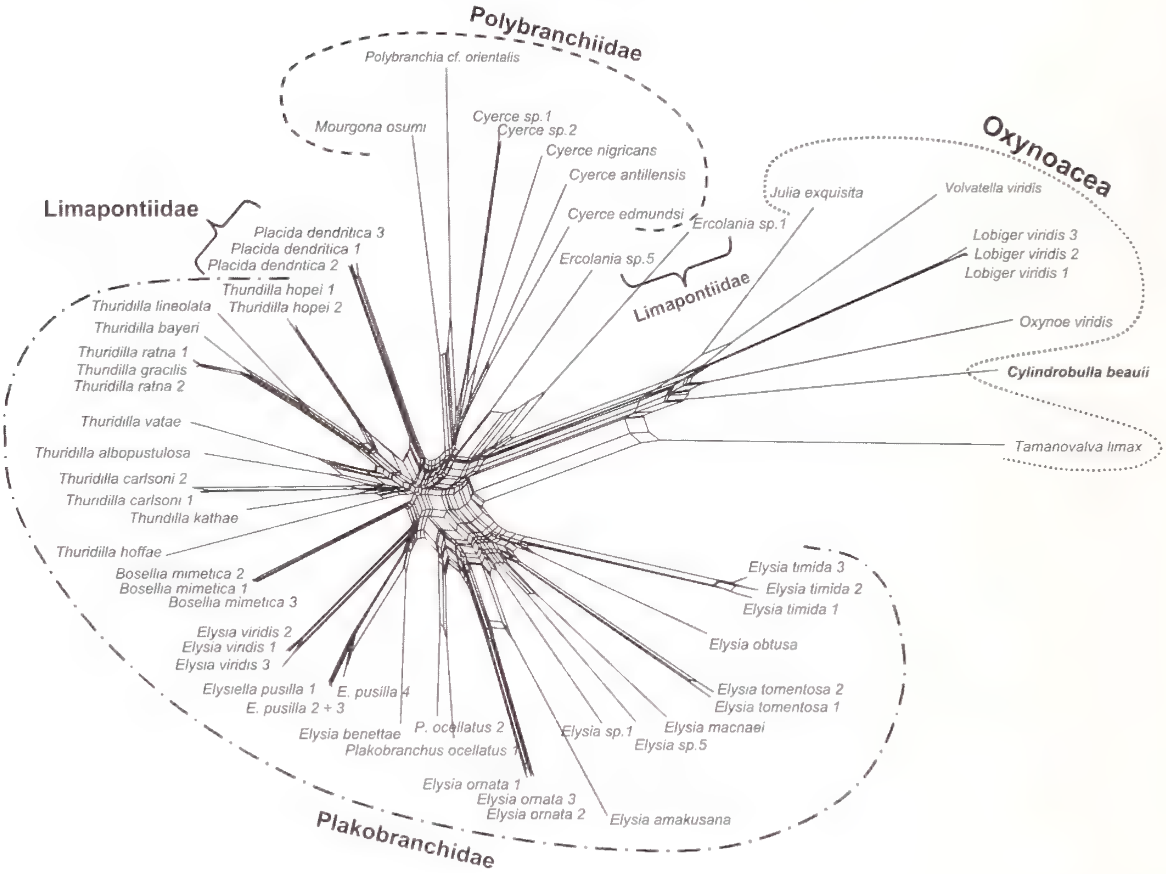
Polybranchiidae
Polybranchia cf. orientalis
Mourgona osumi
Cyerce sp.1
Cyerce sp.2
Cyerce nigricans
Cyerce antillensis
Cyerce edmundsi
Ercolania sp.1
Ercolania sp.5
Limapontiidae
Oxynoacea
Julia exquisita
Volvatella viridis
Lobiger viridis 3
Lobiger viridis 2
Lobiger viridis 1
Oxynoe viridis
Cylindrobulla beauii
Tamanovalva limax
Limapontiidae
Placida dendritica 3
Placida dendritica 1
Placida dendritica 2
Thuridilla hopei 1
Thuridilla lineolata
Thuridilla hopei 2
Thuridilla bayeri
Thuridilla ratna 1
Thuridilla gracilis
Thuridilla ratna 2
Thuridilla vatae
Thuridilla albopustulosa
Thuridilla carlsoni 2
Thuridilla carlsoni 1
Thuridilla kathae
Thuridilla hoffae
Bosellia mimetica 2
Bosellia mimetica 1
Bosellia mimetica 3
Elysia viridis 2
Elysia viridis 1
Elysia viridis 3
Elysiella pusilla 1
E. pusilla 4
E. pusilla 2 + 3
Elysia benettae
P. ocellatus 2
Plakobranchus ocellatus 1
Elysia ornata 1
Elysia ornata 3
Elysia ornata 2
Elysia sp.1
Elysia macnaei
Elysia sp.5
Elysia amakusana
Elysia timida 3
Elysia timida 2
Elysia timida 1
Elysia obtusa
Elysia tomentosa 2
Elysia tomentosa 1
Plakobranchidae

Fig. 5. Sacoglossa; Neighbor network analysis applying SplitsTree4 to visualize conflict in the whole sacoglossan data set. Parallel edges with same length indicate a split and visualize the distances between the two groups involved. Note the long edges between the Plakobranchacea and the Oxynoacea + *Cylindrobulla*. Fit value: 95,85.

sal surface. MARCUS DU BOIS-REYMOND (1980) and later THOMPSON and JAKLIN (1988) positioned *Bosellia* in the family Plakobranchidae, but MARCUS DU BOIS-REYMOND (1982) transferred it in its own family Boselliidae based on the difference in number of chromosomes in *Bosellia* (n=7) and other sacoglossans (n=17), as well as the lack of parapodia. JENSEN (1996) criticized that the number of chromosomes is only known for the species *Bosellia mimetica* and not for other species of this genus but decided to retain the family status until the phylogenetic position of the genus is solved. According to our results, *Bosellia* seems to represent an own evolutionary line, independent of the family Plakobranchidae (with the genera *Elysia*, *Thuridilla* and *Plakobranchus)*, but its position varies within the Plakobranchacea. The result of the Maximum Likelihood analysis places *Bosellia* as sistertaxon of Plakobranchidae, similar to the results obtained by JENSEN (1996). BASS and KARL (2006) used *Bosellia mimetica* and *Bosellia marcusi* in their phylogenetic analysis of Plakobranchidae. Similar to our results, *B. mimetica* forms the sister taxon to the further included genera *Elysia*, *Elysiella*, *Plakobranchus* and *Thuridilla*. But the other included member of *Bosellia*, *B. marcusi,* represents the sistertaxon to *Elysia timida*. The authors considered a wrong determination of their animal.

The family Plakobranchidae appears monophyletic only in the Maximum Likelihood analysis. This is in accordance with JENSEN's analysis (1996). She mentioned as most important autapomorphies the parapodia in which the digestive gland and the reproduction system reach. In the SplitsTree analysis support of the split Plakobranchidae versus rest of Sacoglossa is not found at all. Within the Plakobranchidae, the genus *Thuridilla* is monophyletic in the NJ- and ML-analysis and branching pattern is identical. The Bayesian analysis produced two of these monophyletic *Thuridilla* complexes but could not resolve their positions in detail. Also in the Splits analysis, no split *Thuridilla*/rest of Sacoglossa is visible. GOSLINER (1995: 45) mentioned following apomorphic features: „elongate rhinophores, single, thick, darkly pigmented ampulla, nonmuscular, unarmed penis, bursa copulatrix with seperate gonopore and orange or red eggs.“ A darkly pigmented ampulla could not be confirmed in the Mediterranean *Thuridilla hopei* (own unpublished data). It is possible that only Indopacific species have a pigmented ampulla, since Gosliner dealt with these species. *Elysia viridis* also lays „reddish yellow“ eggs when feeding on *Chaetomorpha* (TROWBRIDGE & TODD 2001: 222). One particular clade was found in all analysis: (*T. bayeri* (*T. ratna* 2 (*T. ratna* 1 /*T. gracilis*))). The species are only distinguished by different colouration (GOSLINER 1995). JENSEN (1992: 278) found „slight differences in the size of the pharyngeal pouch.“ BRODIE and BRODIE (1990) considered *T. bayeri* as synonym with *T. ratna*. GOSLINER (1995: 9) mentioned that “Internally, there is little difference between *Thuridilla bayeri* [and] *Thuridilla ratna*“, “... these data strongly suggest that the described differences between *T. bayeri* and *T. ratna* are simply variations within a single species that is extremely variable in its colouration.“ Concerning *Thuridilla gracilis*, GOSLINER (1995) complained about the insufficient description of Risbec in 1928, hampering a correct assignment. RUDMAN (2000) stated that “Contrary to Gosliner (1995), I consider *T.bayeri* to be a synonym of *Thuridilla gracilis*.“ Our study supports the synonymisation of *T. ratna* with *T. gracilis* Risbec, 1928. But synonymisation of *Thuridilla bayeri* with *Thuridilla gracilis* seems preliminary, since we have no information on intraspecific variability of the gene. According to our splits analysis, there are affiliations also between *T. bayeri* and *T. lineolata* (Fig. 7). Comparison of GOSLINER´s data (1995) with our data is hardly possible due to small overlap of included species. In agreement is the sister taxa relationship of *Thuridilla vatae* and *Thuridilla albopustulosa*.

JENSEN (1997a) estimated the number of *Plakobranchus*-species from 1 to 14. In this study two specimens of *Plakobranchus ocellatus* were used. Although all analyses published yet (GOSLINER 1995; JENSEN 1996; BASS & KARL 2006) assign *Plakobranchus* to other members of the family Plakobranchidae, its position varies considerably. A unique character of the genus in relation to other members of Plakobranchidae is the dorsal position of the anus (JENSEN 1992).

In all analyses on Plakobranchidae (JENSEN 1996; BASS & KARL 2006; this study), *Elysiella pusilla* is always located among *Elysia* species, *E. benettae* usually forming its sistertaxon. JENSEN and WELLS (1990: 324) emphasized the validity of an own genus *Elysiella*: “this species shows so many differences from other species of *Elysia* that it definitely belongs to a different genus.“ But all phylogenetic analyses indicate the invalidity of this genus, there-

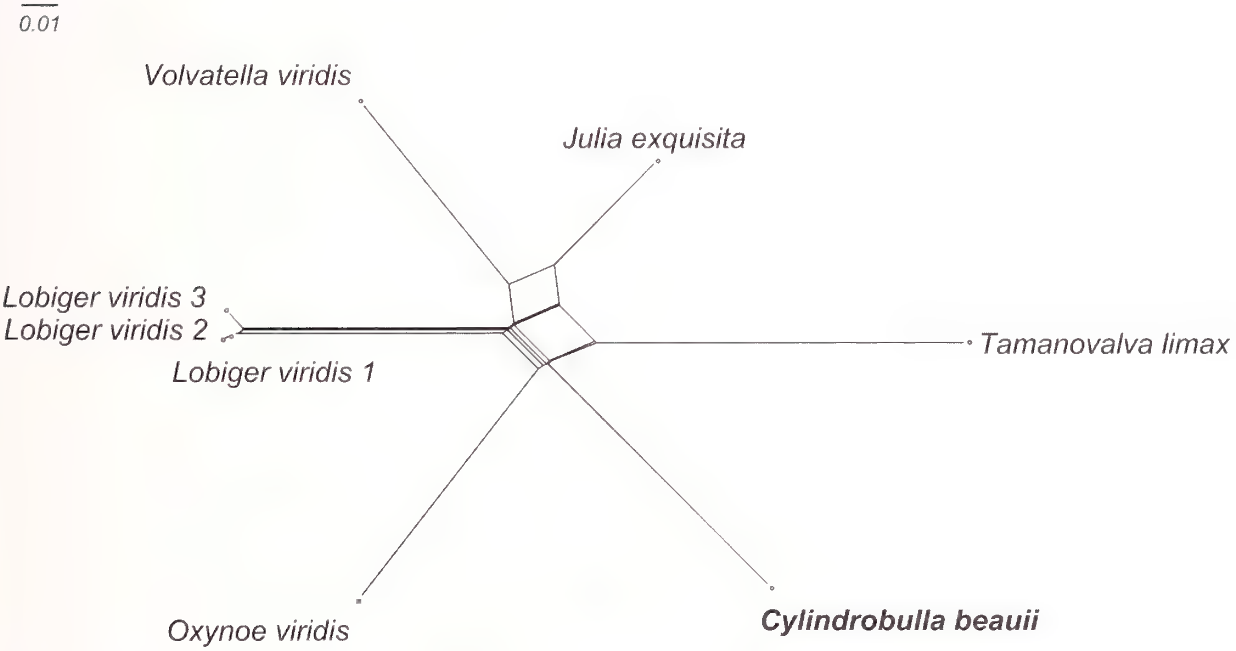

Fig. 6. Neighbor network analysis applying SplitsTree4 to visualize conflict in the reduced data set, comprising only Oxynoacea and the outgroup taxon *Cylindrobulla beauii*. Note that there is no split separating *Cylindrobulla beauii* from the Oxynoacea. Similar long edges connecting *Volvatella*, *Julia* and *Tamanovalva* indicate the lack of signal of the taxon Juliidae. Fit value: 98,53.

fore *Elysiella pusilla* is named from hereon as *Elysia pusilla* (Bergh, 1872). Several species, described under the genus name *Elysia* (*Elysia dubia* Eliot, 1904, *Elysia halimedae* Macnae, 1954, *Elysia latipes* Marcus & Marcus, 1960 and *Elysia macnaei* Marcus, 1982) are mentioned to be synonymous to *Elysia pusilla* (see JENSEN & WELLS 1990). MARCUS DU BOIS-REYMOND (1980) distinguished material identified as *Elysia halimedae* by Baba (1957) and Burn (1972) from the original *E. halimedae* Macnae, 1954 from South Africa by the presence of papillate rhinophores in the latter. She re-named the material misidentified as *E. halimedae* and established the name *E. macnaei* Marcus, 1980. Our study includes a specimen from the Zoologische Staatssammlung München, collected in Sulawesi and identified by courtesy by Michael Schrödl as *E. macnaei*. This specimen does not group with *Elysia pusilla* indicating that *E. macnaei* is not synonymous with *E. pusilla*.

Comparing our results with the only available phylogenetic hypothesis on Sacoglossa elaborated by JENSEN (1996), the results of the Maximum Likelihood analysis come closest to her results. Both analyses support monophyly of the Plakobranchacea, Plakobranchoidea, Plakobranchidae as well as the genera *Elysia* (with *Elysiella* as a synonym) and *Thuridilla*. *Plakobranchus* and *Bosellia* form distinct evolutionary lines. Juliidae are also monophyletic. The two hypotheses contradict in the paraphyly (this study) versus monophyly (JENSEN 1996) of the Oxynoacea, Oxynoidae and Limapontiidae. But it has to be emphasized that these taxa are underrepresented in our study and future analyses have to be performed with more representatives of these groups. Furthermore, other genes have to be used for analysing deeper nodes of Sacoglossa, since the 16Sr DNA gene (this study), as well as the CO1 gene (unpublished results) show saturation on higher level.

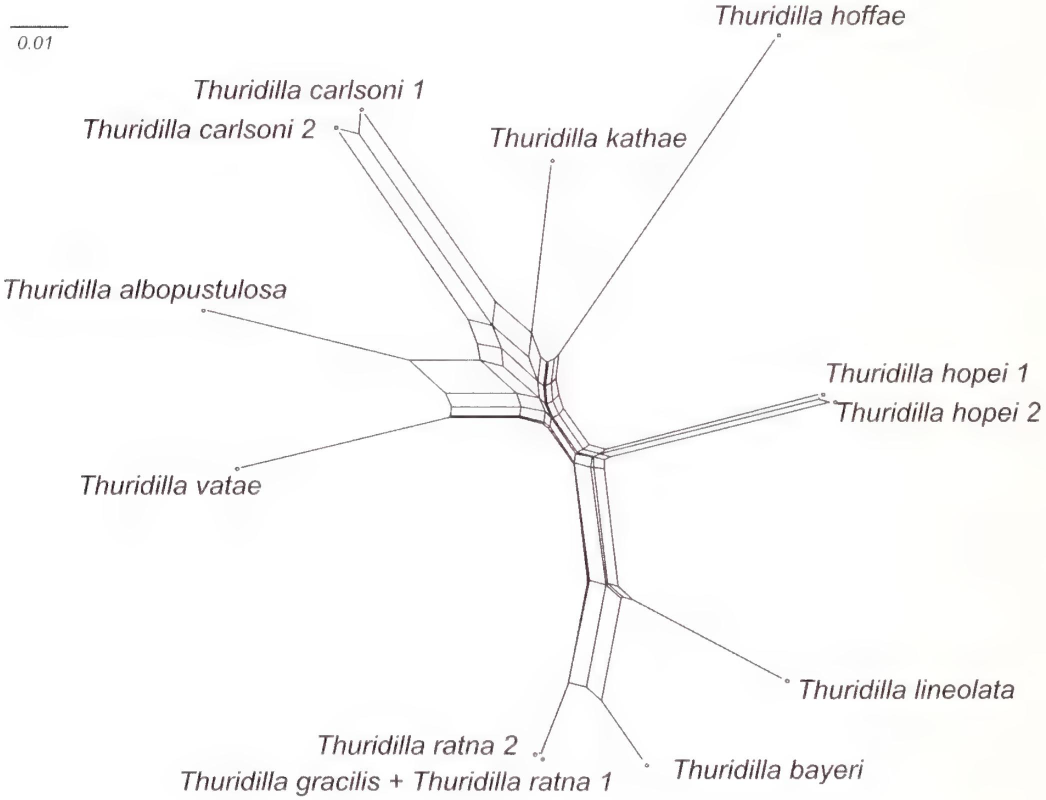

Fig. 7. Neighbor network analysis applying SplitsTree4 to visualize similarity of species in a reduced data set, comprising only members of the genus *Thuridilla*. Note the one edge leading to the 2 specimens of *Thuridilla ratna* and the one specimen of *T. gracilis*. No conflict occurs, indicating the synonymy of these 2 species. *Thuridilla bayeri* is separate, nevertheless the long edges characterizing the split *Thuridilla gracilis /T. ratna /T. bayeri* indicate its closer affinity to *T. gracilis*, than the shorter edge characterizing the split *T. bayeri/T. lineolata*. Fit value: 98,12.

4.2. Food spectrum of Sacoglossa

Several authors emphasized that sacoglossans have a very narrow food spectrum (e.g. Thompson 1964; Clark 1975, 1994). However, the contrary was also stated: „..., some species feed on several different food items (...), and food spectra are not so narrow as previously assumed.“ (Jensen 1980a: 73). „Tropical Ascoglossa are relatively non-specific feeders, possibly because of the higher diversity of (see Table 2) foods in tropical seas.“ (Clark & Busacca 1978: 281). That food spectrum varies in different taxa is evident in the genus *Elysia* with species feeding exclusively on one food species (e.g. *Elysia translucens* on *Flabellia* (former *Udotea*) *petiolata*, see Marín & Ros 2004) or on a high variety of food species belonging to completely different phyla (e.g. *Elysia crispata* feed-

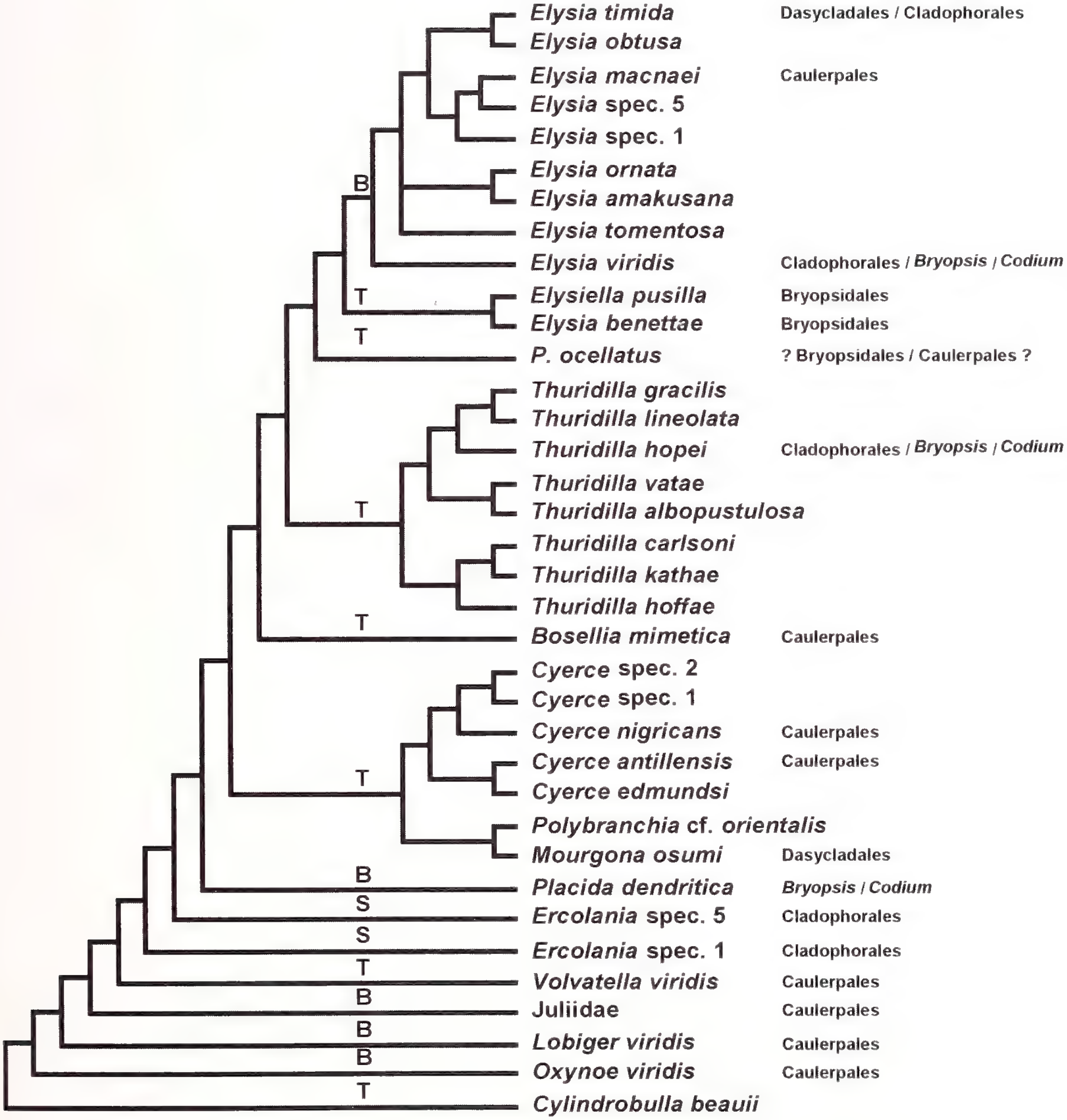
Elysia timida
Dasycladales / Cladophorales
Elysia obtusa
Elysia macnaei
Caulerpales
Elysia spec. 5
Elysia spec. 1
B
Elysia ornata
Elysia amakusana
Elysia tomentosa
Elysia viridis
Cladophorales / Bryopsis / Codium
T
Elysiella pusilla
Bryopsidales
Elysia benettae
Bryopsidales
T
P. ocellatus
? Bryopsidales / Caulerpales ?
Thuridilla gracilis
Thuridilla lineolata
Thuridilla hopei
Cladophorales / Bryopsis / Codium
Thuridilla vatae
T
Thuridilla albopustulosa
Thuridilla carlsoni
Thuridilla kathae
Thuridilla hoffae
T
Bosellia mimetica
Caulerpales
Cyerce spec. 2
Cyerce spec. 1
Cyerce nigricans
Caulerpales
Cyerce antillensis
Caulerpales
T
Cyerce edmundsi
Polybranchia cf. orientalis
Mourgona osumi
Dasycladales
B
Placida dendritica
Bryopsis / Codium
S
Ercolania spec. 5
Cladophorales
S
Ercolania spec. 1
Cladophorales
T
Volvatella viridis
Caulerpales
B
Juliidae
Caulerpales
B
Lobiger viridis
Caulerpales
B
Oxynoe viridis
Caulerpales
T
Cylindrobulla beauii

Fig. 8. Phylogeny of Sacoglossa (redrawn after the Maximum Likelihood phylogram, see Fig. 3) with food (higher taxa level) and tooth form mapped on the tree. T Triangular shaped teeth, S sabot shaped teeth, B blade shaped teeth.

ing on the siphonalean heterokontophyte *Vaucheria*, the siphonocladalean *Chaetomorpha* (Cladophorales), the siphonalean *Batophora* (Dasycladales), on different siphonalean Halimedales and members of the taxon Bryopsidales). In few species, an ontogenetic food switch is described, (e.g. juvenile *Elysia timida* feeds on *Cladophora dalmatica,* adults on *Acetabularia acetabulum* (MARÍN & ROS 1993)).

Oxynoacea, representing about 20% of Sacoglossa (JENSEN 1997a), exclusively feed on the genus *Caulerpa*. Members of the Caulerpales with xylan in the cell wall remain the main food source of sacoglossans, even in the highly evolved Plakobranchidae (see Table 2). Some plakobranchids do not feed solely on Caulerpales, but seem to forage additionally on Cladophorales, which have cellulose in their cell wall. *Ercolania* and other limapontiids have switched to the Cladophorales as the main food source, Hermaeidae focus on Rhodophyta, and few sacoglossans are oophagous (consuming eggs of other opisthobranchs). A switch to Dasycladales with mannan in the cell wall is seldom (e.g. *Elysia timida*, *E. filicauda*) and for these species other food sources (Caulerpales) are also recorded. Only species of *Mourgona* seem to focus on Dasycladales.

JENSEN (1997a) assumed that the evolution of the sacoglossans was linked to the structure of cell walls in their food organisms. Within evolution of Plakobranchacea, members of this taxon could only change their food spectrum from Caulerpales and Udoteacea (containing xylan) to Codiales and Dasycladales (with mannan) or Cladophorales/Siphonocladales (with cellulose) by exploring Derbesiales (actual taxonomy: Bryopsidales) with cell walls of xylan in the haplonts and cell walls of mannan in the diplonts. According to JENSEN (1993a), 12% of the sacoglossans are able to feed on several algal species with different cell wall structure. She described populations of *Elysia viridis* feeding on *Chaetomorpha* (Cladophorales) with cell walls containing cellulose and populations on *Codium* (Bryopsidales) with cell walls containing mannan (JENSEN 1989a). In experiments, she transferred *Elysia viridis* collected from *Codium* to *Chaetomorpha* and *vice versa*. Some specimens accepted the other algal species but still preferred the one that was their original food.

In choice experiments, TROWBRIDGE and TODD (2001) confirmed this behaviour of possible food switch. They showed that *E. viridis* collected on the native food *Cladophora rupestris* preferred this alga, but were able to switch to introduced species of *Codium fragile* ssp *tomentosoides* and *C. fragile* ssp. *atlanticum*. They also demonstrated that the F1 generation also preferred *C. fragile* in laboratory experiments, independent whether the parents were cultivated on *Cladophora rupestris* or *Codium fragile*. Juveniles grew faster on the introduced species. They concluded, that "slug performance is much better on the introduced host *Codium fragile* than on native *Cladophora*." (TROWBRIDGE & TODD 2001: 234).

4.3. Food spectrum and tooth shape

BLEAKNEY (1990) detected different types of teeth in *Placida dendritica* in correlation with different kinds of food. JENSEN (1993a, 1997a) also found a positive correlation of tooth shape and algal diet. Within Oxynoacea (feeding exclusively on *Caulerpa*) the plesiomorphic triangular shaped tooth occurs as well as the blade-shaped tooth form. The triangular type is only found in those species, which feed on algae with xylan or mannan in the cell wall, but not cellulose. The blade-shaped tooth evolved several times within Sacoglossa, and this tooth type seems to be adapted for feeding on all types of algae. Only the sabot-shaped tooth seems to be restricted to those species mainly feeding on algae with cellulose. In an experiment JENSEN (1993a) could show that phenoplastic variation of teeth underlies environmental factors. *Elysia viridis* collected from *Codium* (Bryopsidales with mannan) was offered *Chaetomorpha* (Cladophorales with cellulose) as only food source for one year. The newly formed teeth in the upper limb of the radula were similar to those teeth of *Elysia viridis* specimens collected from *Chaetomorpha.* Mapping tooth shape and algal food on the cladogram obtained by the ML analysis (Fig. 8) does not reveal correlation of slug evolution and tooth shape, nor toothshape in correlation with consumed algal taxon.

4.4. Food spectrum and phylogeny

Based on her phylogenetic hypothesis, JENSEN (1997a) postulated that the ancestor of the Sacoglossa foraged on a filamentous calcified member of the udoteacean *Halimeda* (Caulerpales), since all basal Plakobranchacea are feeding on this type of algae. The monophyletic Oxynoacea switched to the uncalcified genus *Caulerpa*, on which the shelled sacoglossans exclusively feed. In this hypothesis, JENSEN (1997a) assumed that *Cylindrobulla* also feeds on *Halimeda,* which would strengthen her hypothesis. But this was never observed. Actually, her note that "*Cylindrobulla* is apparently associated with the non-photosynthetic, uncalcified rhizoids of *Halimeda* " (JENSEN 1997a: 319) could indicate that *Cylindrobulla* forages on epibenthic algae associated with *Halimeda*. Her description on tooth morphology (JENSEN 1989b), as well as the lack of a suctorial pump (JENSEN 1996, 1997a) also suggests grazing as a feeding mode, and not piercing cell walls and sucking out the cytoplasmatic contents. According to our analysis and the resulting phylogenetic hypothesis, another evolutionary scenario can be discussed, in which uncalcified *Caulerpa* is the original food source of Sacoglossa. This conforms to the hyptheses of CLARK & BUSACCA (1978), JENSEN (1980a) and CLARK & DE FREESE (1987). *Caulerpa* seems to be attractive even for sacoglossans that do not feed on that genus *in situ*. In experiments, JENSEN (1988) demonstrated that many slugs chose a cell homogenate of *Caulerpa* as food. But mapping radula morphology as described by JENSEN (1996) on our cladogram (Fig. 8) produces incongruencies especially concerning the re-evolution of the triangular tooth shape.

Fossil records of Sacoglossa are rare, but shelled Juliidae have been recorded from the Oligocene (JANSSEN 1979). JENSEN (1997a) dated back the origin of Sacoglossa in the Cretaceous because the fossil record of the calcified *Halimeda* dates back so far. She further noted that Sacoglossa then had to exist before the origin of *Halimeda* itself. We do not follow this statement since *Halimeda* could have existed long before the first sacoglossan slug evolved and foraged on this particular food. CLARK & DE FREESE (1987) hypothesized that *Halimeda* was already calcified when the first sacoglossan appeared and that feeding did not influence the grade of calcification significantly. In contrast, JENSEN (1997a) assumed an increasing calcification as a mechanical defense of the alga as an answer to predation by Sacoglossa and the adaptation of the buccal apparatus of Sacoglossa to deal with this mechanical defense. Calcification does not only appear in algae predated by Sacoglossa but is a wide spread phenomenon in Rhodophyta or Phaeophyceae since it gives mechanical stability in areas with strong current or strong swell (e.g. dictyoalean *Padina pavonica,* Corallinacea, etc.). The mediterranean Coralligène is produced mainly by the red alga *Mesophyllum alternans* and *Lithophyllum frondosum* with a high calcification rate and no recorded predation (BALLESTEROS 2006).

4.5. Conclusions

In future analyses, more taxa especially of the Oxynoacea and Limapontioidea have to be included to test the two different hypotheses presented by JENSEN (1996) based on morphology and the one outlined earlier by other authors and the present study based on molecular markers. Since both mitochondrial genes, 16Sr DNA (presented here) and CO1 (not included in this study), show a high substitution rate already on higher taxa level, genes with lower evolutionary rates, e.g. nuclear genes as 18S and 28S, have to be analysed additionally. Further investigation on food organisms is also needed to analyse a possible co-evolution of slugs and algae. This can only be done with a rigorous identification of ingested algae, e.g. by analysing algal chloroplast genes in the slugs, which would exclude those algae used only as substrat.

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Addendum: After receiving the proofs, Grzymbowski et al. 2007 was published, and a name for *Ercolania* spec. 1 is available now. The species is called *Ercolania kencolesi* Grzymbowski, Stemmer & Wägele, 2007.

Table 1. Specimens used in the phylogenetic analysis with accession numbers. ZSM Zoologische Staatssammlung Munich.

Family	Taxon	Origin	Accession number
outgroup			
	Cylindrobullidae Thiele, 1931 P. Fischer, 1856	*Cylindrobulla beauii* Miama, 03-2005	EU140897
OXYNOACEA			
Volvatellidae Pilsbry 1895	*Volvatella viridis* Hamatani, 1976	South Island, Lizard Island/Australia, 12-07-2006	EU140890
Juliidae E.A. Smith 1885	*Julia exquisita* (Gould, 1862)	South Island, Lizard Island/Australia, 11-07-2006	EU140895
	Tamanovalva limax Kawaguti & Baba, 1959	Casuarina Beach, Lizard Island/Australia, 13-07-2006	EU140896
Oxynoidae H. Adams & A. Adams 1854	*Oxynoe viridis* (Pease, 1861)	South Island, Lizard Island/Australia, 10-07-2006	EU140891
	Lobiger viridis 1 Pease, 1863	Lizard Island/Australia, 10-07-2006	EU140892
	Lobiger viridis 2 Pease, 1863	Fiji Island, 26-08-2006 (ZSM 20061650)	EU140893
	Lobiger viridis 3 Pease, 1863	Coconut Beach, Lizard Island/Australia, 12-08-2006	EU140894
PLAKOBRANCHACEA			
Plakobranchoidea			
Boselliidae Marcus 1982	*Bosellia mimetica* 1 Trinchese, 1891	Baretta del Abre near Mataró/Spain, 23-05-2006	EU140872
	Bosellia mimetica 2 Trinchese, 1891	Banyuls-sur-mer/Southern France, 11-05-2006	EU140873
	Bosellia mimetica 3 Trinchese, 1891	Tossa/Spain, 29-08-2003	EU140874
Plakobranchidae Rang 1829	*Elysia amakusana* Baba, 1955	Lizard Island/Australia, 04-03-2005	EU140851
	Elysia benettae Thompson, 1973	Samoa, 06-08-2005 (ZSM 20060293)	EU140868
	Elysia macnaei Marcus E. duB.-R., 1980	NW-Sulawesi/Indonesia, 23-07-2003 (ZSM 20033821)	EU140854
	Elysia obtusa Baba, 1938	Samoa, 20-08-2005 (ZSM 20060257)	EU140860
	Elysia ornata 1 (Swainson, 1840)	Lizard Island/Australia, 09-2002	EU140849
	Elysia ornata 2 (Swainson, 1840)	North Point, Lizard Island/Australia, 14-07-2006	EU140850
	Elysia ornata 3 (Swainson, 1840)	Lizard Island/Australia, 18-03-2005	EU140848
	Elysia timida 1 (Risso, 1818)	Banyuls-sur-mer/Southern France, 02-05-2006	EU140857
	Elysia timida 2 (Risso, 1818)	near Roses/Spain, 22-05-2006	EU140858
	Elysia timida 3 (Risso, 1818)	near Tossa/Spain, 25-05-2006	EU140859
	Elysia tomentosa 1 Jensen, 1997	Lizard Island/Australia, 13-09-2004	EU140852
	Elysia tomentosa 2 Jensen, 1997	Lizard Island/Australia, 21-03-2005	EU140853

Family	**Taxon**	**Origin**	**Accession number**
	Elysia viridis 1 (Montagu, 1804)	Roscoff/Bretagne, Northern France, 2006	EU140861
	Elysia viridis 2 (Montagu, 1804)	Tossa/Spain, 19-05-2006	EU140862
	Elysia viridis 3 (Montagu, 1804)	Banyuls-sur-mer/Southern France, 06-05-2006	EU140863
	Elysia spec.1 (see WÄGELE et al. 2006)	Lizard Island/Australia, 25-07-2005	EU140856
	Elysia spec. 5	South Island, Lizard Island/Australia, 24-07-2006	EU14085
	Elysiella pusilla 1 Bergh, 1872	Maledives, 04-2006	EU140864
	Elysiella pusilla 2 Bergh, 1872	Maledives, 04-2006	EU140866
	Elysiella pusilla 3 Bergh, 1872	Maledives 04-2006	EU140865
	Elysiella pusilla 4 Bergh, 1872	South Island, Lizard Island/Australia, 10-07-2006	EU140867
	Plakobranchus ocellatus 1 Van Hasselt, 1824	Lizard Island/Australia, 21-03-2005	EU140875
	Plakobranchus ocellatus 2 Van Hasselt, 1824	Lizard Island/Australia, 21-03-2005	EU140876
	Thuridilla albopustulosa Gosliner, 1995	NW-Sulawesi/Indonesia, 17-07-2003 (ZSM 20033615)	EU140889
	Thuridilla bayeri (Marcus, 1965)	NW-Sulawesi/Indonesia, 17-07-2003 (ZSM 20033612)	EU140886
	Thuridilla carlsoni 1 Gosliner, 1995	Lizard Island/Australia, 13-09-2004	EU140877
	Thuridilla carlsoni 2 Gosliner, 1995	Lizard Island/Australia, 25-06-2006	EU140878
	Thuridilla gracilis (Risbec, 1928)	Lizard Island/Australia, 18-03-2005	EU140883
	Thuridilla hoffae Gosliner, 1995	Samoa, 16-08-2005 (ZSM 20060224)	EU140880
	Thuridilla hopei 1 (Verany, 1853)	Elba, 07-2001	EU140881
	Thuridilla hopei 2 (Verany, 1853)	Baretta del Abre near Mataró/Spain, 24-05-2006	EU140882
	Thuridilla kathae Gosliner, 1995	Lizard Island/Australia, 13-09-2004	EU140879
	Thuridilla lineolata Bergh, 1905	NW-Sulawesi/Indonesia, 07- 2003	EU140887
	Thuridilla ratna 1 (Marcus, 1965)	Lizard Island/Australia, 25-06-2005	EU140884
	Thuridilla ratna 2 (Marcus, 1965)	Lizard Island/Australia, 13-09-2004	EU140885
	Thuridilla vatae (Risbec, 1928)	Samoa, 11-08-2005 (ZSM 20060088)	EU140888
Limapontioidea			
Polybranchiidae O'Donoghue 1929	*Cyerce antillensis* Engel, 1927	Azores, 09-2001	EU140841
	Cyerce edmundsi (Thompson, 1977)		EU140842
	Cyerce nigricans (Pease, 1866)	Channel, Lizard Island/Australia, 13-07-2006	EU140843

Family	Taxon	Origin	Accession number
	Cyerce spec. 1 (see Wägele et al. 2006)	Lizard Island/Australia, 25-07-2005	EU140845
	Cyerce spec. 2 (see Wägele et al. 2006)	Lizard Island/Australia, 13-09-2004	EU140844
	Polybranchia cf. *orientalis* (Kelaart, 1858)	Lizard Island/Australia, 01-09-2004	EU140846
	Mourgona osumi Hamatani, 1994	North Point, Lizard Island/Australia, 14-07-2006	EU140847
Limapontiidae Gray 1847	*Placida dendritica* 1 (Alder & Hancock, 1843)	Tossa/Spain, 20-05-2006	EU140869
	Placida dendritica 2 (Alder & Hancock, 1843)	Tossa/Spain, 20-05-2006	EU140870
	Placida dendritica 3 (Alder & Hancock, 1843)	Tossa/Spain, 20-05-2006	EU140871
	Ercolania spec.1	Casuarina Beach, Lizard Island/Australia, 02-07-2006	EU140840
	Ercolania spec.5	Casuarina Beach, Lizard Island/Australia, 07-07-2006	EU140839

Table 2. Sacoglossan food organisms compiled from literature.

Species	Food	Reference
OXYNOACEA		
Volvatellidae		
Ascobulla fischeri	*Caulerpa* spp.	Gascoigne & Sartory 1974 after Burn 1972
Ascobulla fragilis	*Caulerpa prolifera*	Marín & Ros 2004
Ascobulla ulla	*Caulerpa racemosa*	Jensen 1980a
	Caulerpa racemosa, **Laboratory**: *Caulerpa sertularoides, Caulerpa cupressoides, Caulerpa verticillata*	Jensen 1981
	Caulerpa racemosa	Clark 1994
Volvatella australis	*Caulerpa*	Jensen 1997b
Volvatella bermudae	*Caulerpa racemosa*	Clark 1994
Volvatella pyriformis	*Caulerpa* spp.	Gascoigne & Sartory 1974 after Burn 1972
Volvatella	*Caulerpa*	Fontana et al. 1999
Juliidae		
Edenttellina typica	*Caulerpa scalpelliformis*	Gonor 1961 after Burn 1960b
	Caulerpa brownii	Burn 1965
	Caulerpa scalpelliformis	Gascoigne & Sartory 1974 after Burn 1972
Berthelinia caribbea	*Caulerpa verticillata*	Edmunds 1963
	Caulerpa verticillata	Jensen 1980a after Grahame 1969
	Caulerpa verticillata	Clark 1994
Berthelinia darwini	*Caulerpa* sp.	Jensen 1997b
Berthelinia ganapati	*Caulerpa racemosa*	Jensen 1980a after Sarma 1975
Berthelinia rottnesti	*Caulerpa simpliciuscula*	Jensen 1993b
	Caulerpa racemosa	Williams & Walker 1999
Julia japonica	*Caulerpa ambigua*	Jensen 1980a after Kawaguti & Yamasu 1966
Midorigai australis	*Caulerpa simpliciuscula*	Gascoigne & Sartory 1974
	Caulerpa simpliciuscula	Jensen 1980a after Burn 1960
Tamanovalva babai	*Caulerpa scalpelliformis, Caulerpa geminata*	Gascoigne & Sartory 1974 after Burn 1972
	Caulerpa scalpelliformis, Caulerpa geminata	Jensen 1980a after Burn 1960, 1965
Tamanovalva limax	*Caulerpa okamurai*	Jensen 1980a after Kawaguti & Baba 1959

Species	Food	Reference
Oxynoidae		
Lobiger serradifalci	*Caulerpa prolifera*	Gonor 1961
	Caulerpa prolifera	Marín & Ros 2004
Lobiger souverbii	*Caulerpa racemosa*	Jensen 1980a
Oxynoe antillarum	*Caulerpa racemosa*	Jensen 1980b
	Caulerpa racemosa, **Laboratory**: *Caulerpa sertularioides*	Jensen 1980a; Jensen 1980a after Marcus & Hughes 1974; Clark & Busacca 1978
Oxynoe azuropunctata	*Caulerpa paspaloides*, *C. cupressoides*, *C. sertularioides*, **Laboratory**: *C. racemosa*	Jensen 1980b
	Caulerpa paspaloides	Clark 1994
Oxynoe olivacea	*Caulerpa prolifera*	Marín & Ros 2004
Oxynoe panamensis	*Caulerpa sertularioides*	Jensen 1980a after Lewin 1970
	Caulerpa sertularioides	Jensen 1993c after Doty & Aguilar-Santos 1970
Oxynoe viridis	*Caulerpa* spp.	Gascoigne & Sartory 1974
Roburnella wilsoni	*Caulerpa*	Jensen 1993b
PLAKOBRANCHACEA		
Plakobranchoidea		
Boselliidae		
Bosellia corinnae	*Halimeda*	Jensen 1993a
Bosellia marcusi	*Halimeda opuntia*	Jensen & Clark 1983
Bosellia mimetica	*Halimeda tuna*	Portmann 1958
	Udotea, *Halimeda*	Thompson & Jaklin 1988
Plakobranchidae		
Elysia atroviridis	*Codium fragile*	Kawaguti & Yamasu 1965
Elysia australis	*Enteromorpha*, *Cladophora*, *Chaetomorpha*	Jensen 1992 after Jensen 1991
	Enteromorpha, *Cladophora*, *Rhizoclonium*	Jensen 1993a
	Acetabularia peniculus, *Chaetomorpha*, *Rhizoclonium*, *Enteromorpha*	Williams & Walker 1999 after Hinde 1983 and after Jensen 1990
Elysia benettae	*Chlorodesmis*	Jensen 1993a
Elysia canguzua	*Codium* sp.	Jensen 1980a after Marcus 1955
	Bryopsis plumosa, *Codium* sp.	Jensen & Clark 1983 after Marcus 1955
	Laboratory: *Chaetomorpha*	Jensen & Clark 1983
Elysia catulus	*Zostera marina*	Clark 1975
Elysia chilkensis	most probably *Enteromorpha*	Jensen 1993c
Elysia chlorotica	*Cladophora* sp.	Franz 1968
	Cladophora spp., *Vaucheria* spp.	Clark 1975
	Chaetomorpha sp.	Jensen & Clark 1983 after West 1977
	Vaucheria litorea	Rumpho et al. 2000 after Mujer et al. 1996 and after Pierce et al. 1996
Elysia crispata	*Halimeda* sp., *Bryopsis plumosa*, *Penicillus* sp., *Batophora oerstedi*	Clark & Busacca 1978
	Halimeda sp., *Bryopsis plumosa*, *Penicillus* sp., *Batophora oerstedi*, *Caulerpa verticillata*	Jensen 1980a
	Laboratory: *Caulerpa verticillata*, *C. racemosa*, *Halimeda discoidea*, *Chaetomorpha* sp.	Thompson & Jarmann 1989
	Vaucheria litorea	Pierce et al. 2003
	Penicillus capitatus, *Halimeda incrassata*, *H. monile*	Curtis et al. 2005 after Curtis et al. 2003
	Bryopsis plumosa, *Derbesia tenuissima*	Curtis et al. 2005
	Bryopsis plumosa	Curtis et al. 2005
Elysia degeneri	*Udotea*	Horgen et al. 2000

Species	Food	Reference
Elysia diomedea	*Padina* sp.	Jensen 1980a after Bertsch & Smith 1973
Elysia evelinae	*Biddulphia* sp., ? *Dictyota*	Jensen 1980a; Jensen 1980a after Marcus 1957
	Biddulphia	Jensen 1993a
Elysia expansa	*Caulerpa*	Jensen 1993b
	Caulerpa racemosa, C. cupressoides	Williams & Walker 1999
Elysia filicauda	? *Acetabularia peniculus*	Jensen & Wells 1990
	Acetabularia	Jensen 1992 after Schmekel 1968 and after Nuttall 1989
	Caulerpa racemosa, C. cupressoides	Williams & Walker 1999
Elysia flava	cf. *Cladophora*	Wägele & Johnson 2001 after Marín & Ros 1988
Elysia flavomacula	**Laboratory**: *Chaetomorpha antennina, Cladophoropsis sp.*	Jensen 1990a
Elysia fusca	*Codium* sp.	Jensen 1980a after Schmekel 1968
Elysia gordanae	*Cladophora* sp.	Wägele & Johnson 2001 after Marín & Ros 1988
Elysia hedgpethi	*Codium fragile, Bryopsis corticulans*	Greene 1970
Elysia japonica	*Chaetomorpha, Cladophoropsis sp.*	Jensen 1993a
Elysia leucolegnote	*Boodleopsis pusilla*	Jensen 1990a, Jensen 1990b
Elysia macnaei	*Halimeda cuneata*	Macnae 1954
	Halimeda macroloba	Paul & Alstyne 1988
Elysia maoria	*Codium*	Jensen 1980a after Reid 1964
	Codium convolutum, Codium fragile ssp. *tomentosoides*	Williams & Walker 1999 after Trowbridge 1995
Elysia ornata	*Bryopsis plumosa*	Jensen 1981
	Bryopsis sp.	Horgen et al. 2000
	Bryopsis sp.	Fontana et al. 2001 after Hamann & Scheuer 1993 and after Hamann et al. 1996
Elysia papillosa	*Penicillus* spp.	Jensen 1980a
	Halimeda ssp., *Penicillus, Udotea flabellum*	Clark 1984
	Penicillus, Udotea, Halimeda	Jensen 1993a
Elysia patagonica	adult: *Codium*	Schrödl 1996
	adult: *Bryopsis plumosa*; veliger: *Nanochloropsis* sp.	Muniain et al. 2001
Elysia patina	*Penicillus, Halimeda*	Jensen 1993a
	Udotea	Clark 1994
Elysia punctata	*Codium* spp.	Macnae 1954
Elysia rufescens	*Bryopsis* sp.	Horgen et al. 2000
	Bryopsis sp.	Fontana et al. 2001 after Hamann & Scheuer 1993 and after Hamann et al. 1996
Elysia serca	*Halodule wrightii, Ulva lactuca*	Jensen 1980a; Jensen 1980a after Horsoe 1956
	Halophila engelmanni, Thalassia testudinum, Halodule wrightii	Jensen 1982
	Syringodium filiforme	Williams & Walker 1999 after Jensen 1983
Elysia subornata	*Caulerpa ashmeadii, C. mexicana, C. paspaloides, C. racemosa*	Clark & Busacca 1978
	Caulerpa ashmeadii, C. racemosa, C. sertularioides, **Laboratory**: *C. cupressoides, C. mexicana, C. paspaloides*	Jensen 1980a
Elysia thompsoni	*Caulerpa*	Jensen 1993b

Species	**Food**	**Reference**
Elysia timida	*Codium*	Kremer & Janke 1988
	Acetabularia acetabulum	Marín & Ros 1992
	juvenil: *Cladophora dalmatica*, adult: *Acetabularia acetabulum*	Marín & Ros 1993
Elysia translucens	*Flabellia* (as *Udotea*) *petiolata*	Marín & Ros 2004
Elysia trisinuata	*Codium*	Jensen 1992
Elysia tuca	*Halimeda* spp., *Caulerpa sertularioides*, *C. mexicana*, *C. racemosa*, *Avrainvillea nigricans*, *Udotea* sp.	Clark & Busacca 1978
	Halimeda discoidea	Stirts & Clark 1980
	Halimeda discoidea, *H. incrassata*	Waugh & Clark 1986
	Halimeda incrassata	Clark & DeFreese 1987
	Halimeda incrassata	Clark 1994
Elysia viridis	*Codium tomentosum*	Taylor 1968
	Codium	Bouchet 1984
	Codium fragile	Trench et al. 1973
	Codium tomentosum	Thompson & Jaklin 1988
	Codium, *Chaetomorpha*	Jensen 1989a
	Codium spp., *Bryopsis plumosa*, *Chaetomorpha linum*	Jensen 1980a; Jensen 1980a after Fretter 1941 and after Rasmussen 1973; Jensen 1994 after Jensen 1990
	Codium tomentosum, *Bryopsis* spp., *Cladophora rupestris*	Trowbridge & Todd 2001
Elysiella pusilla	*Halimeda* spp.	Rudman 2003 after Jensen 2003
Plakobranchus ocellatus	**Laboratory**: *Udotea*, *Chlorodesmis*	Jensen 1980a after Switzer-Dunlap 1975
	Laboratory: *Udotea javensis*, *Bryopsis* sp.	Hirose 2005 after Adachi 1991
Pattyclaya arena	*Caulerpa* spp.	Jensen 1992
Pattyclaya brycei	*Caulerpa* spp.	Jensen 1992
Thuridilla hopei	*Derbesia tenuissima*	Marín & Ros 2004
	Derbesia tenuissima	Cimino & Ghiselin 1998 after Gavagnin et al. 1994b
	Cladophora vagabunda	Wägele & Johnson 2001 after Marín & Ros 1988, 1989
Limapontioidea		
Polybranchiidae		
Caliphylla mediterranea	*Bryopsis plumosa*	Brüel 1904
	Bryopsis	Clark & Busacca 1978
	Bryopsis	Gascoigne 1979
	Bryopsis plumosa	Marzo, di et al. 1993
Cyerce antillensis	*Penicillus* spp., *Halimeda* spp.	Jensen 1980a
	Penicillus, *Udotea*, *Halimeda*	Jensen 1993
	Penicillus dumetosus, *Halimeda* ssp.	Clark 1994
Cyerce nigra	*Chlorodesmis comosa*	Miller 1969
Cyerce nigricans	*Chlorodesmis fastigiata*	Hay et al. 1989
	Chlorodesmis	Cimino & Ghiselin 1998 after Roussis et al. 1990
Mourgona germaineae	*Cymopolia barbata*	Jensen 1981
	Cymopolia barbata	Clark 1994
Mourgona osumi	*Acetabularia ryukyuensis*	Hamatani 1994
Polybranchia viridis	? *Caulerpa* spp.	Jensen 1980a after Bertsch & Smith 1973
	Caulerpa racemosa	Clark 1994
Hermaeidae		
Aplysiopsis enteromorphae	*Chaetomorpha* sp., *Cladophora*, *Urospora*, *Rhizoclonium*	Trowbridge 1993
Aplysiopsis formosa	*Cladophora prolifera*	Jensen 1995

Species	Food	Reference
Aplysiopsis smithi	*Rhizoclonium* sp., *Cladophora* sp.,	Jensen 1980a after Gonor 1961;
	Chaetomorpha sp., *Urospora* sp.	Jensen 1980a after Greene 1970
Aplysiopsis zebra	*Cladophora*	Jensen 1993a
	Cladophora fuliginosa, Chaetomorpha	Williams & Walker 1999 after Jensen 1983
Hermaea bifida	*Griffithsia*	Graham 1955 after Pelseneer 1935
	Griffithsia, Delesseria, Heterosiphonia	Taylor 1968
	Griffithsia flosculosa	Taylor 1971
	Griffithsia flosculosa	Kremer & Schmitz 1976
	Bornetia secundiflora	Kremer & Schmitz 1976
		after Cornet & Marche-Marchad 1951
Hermaea cruciata	*Griffithsia* sp.	Jensen & Clark 1983
	Griffithsia	Jensen 1993a
	Griffithsia, Dasya	Williams & Walker 1999 after Jensen 1983
Hermaea evelinemarcusae	*Griffithsia* cf. *ovalis*	Jensen 1993b
Hermaea vancouverensis	*Isthmia nervosa*	Williams & Gosliner 1973
Costasiellidae		
Costasiella nonatoi	*Avrainvillea*	Jensen 1993a
Costasiella ocellifera	*Avrainvillea nigricans*	Clark & Busacca 1978
	Avrainvillea nigricans	Jensen 1980a
	Avrainvillea, **Laboratory**: *Caulerpa fastigiata*	Jensen 1981
	Avrainvillea nigricans	Clark et al. 1981
	Avrainvillea	Clark 1984
	Avrainvillea nigricans, *Caulerpa fastigiata, Cladophora*	Williams & Walker 1999 after Jensen 1980, 1981, 1983
	Avrainvillea	Jensen 1993a
	Avrainvillea nigricans	Clark 1994
Costasiella pallida	*Vaucheria vipera*	Jensen 1990a, 1990b
Limapontiidae		
Alderia modesta	*Vaucheria* spp.	Evans 1953
	Vaucheria, Rhizoclonium	Graham 1955 after Gascoigne 1954
	Vaucheria spp.	Clark 1975
	Vaucheria spp.	Jensen 1980a after Hartog 1959
	Vaucheria longicaulis	Krug & Manzi 1999
Calliopaea oophaga	Eggs of *Philine denticulata*, **Laboratory**: eggs of *Polycera quadrilineata*, *Alderia modesta*, *Ercolania nigra*, *Limapontia capitata*, *Retusa truncatula*, *Turritella communis*	Jensen 1986
	Eggs of *Philine denticulata* and *Retusa truncatula*	Lemche 1974 (Appendix of Gascoigne & Sartory 1974)
Ercolania boodleae	*Chaetomorpha aerea*, *C. moniligera*, *Cladophora* spp.	Jensen 1980a after Usuki 1977
Ercolania coerulea	*Valonia* sp.	Jensen 1980a after Schmekel 1968
	Valonia sp., *Dictyosphaeria cavernosa*, juvenile: *Cladophoropsis* sp.	Jensen 1981
	Dictyosphaeria, *Valonia*, *Cladophoropsis*	Jensen 1993a
Ercolania emarginata	*Chaetomorpha, Cladophoropsis*	Jensen 1993a
Ercolania endophytophaga	*Struvea plumosa* (native), **Laboratory:** *Valonia* spec.	Jensen 1999
Ercolania fuscata	*Cladophora* spp., *Chaetomorpha linum*	Clark 1975
Ercolania gopalai	*Chaetomorpha* sp.	Jensen 1980a after Rao 1937
Ercolania nigra	*Chaetomorpha linum*	Jensen 1980a; Jensen 1980a after Rasmussen 1973
Ercolania translucens	*Rhizoclonium*	Jensen 1997b
Ercolania vanellus	? *Caulerpa verticillata*	Jensen 1980a after Edmunds 1963

Species	Food	Reference
Ercolania viridis	*Chaetomorpha* sp.	Jensen 1980a after Trinchese 1872
	Chaetomorpha spp., *Cladophora* spp.	Jensen 1980a
	Chaetomorpha linum	Marín & Ros 1992 after Marín & Ros 1988
	Chaetomorpha, Cladophora, Cladophoropsis	Jensen 1993a, Jensen 1981
	Chaetomorpha capillaris, Chaetomorpha linum	Marzo, di et al. 1993
Ercolania spec.1	*Boergesenia* cf. *forbesii*	Grzymbowski et al. 2007
Ercolania spec.5	*Boodlea* sp.	Unpublished data HW
Ercolania sp. (Clark 1994)	*Cladophoropsis*	Clark 1994
Limapontia capitata	*Cladophora arcta, Enteromorpha*	Graham 1955 after Gascoigne 1952
	Cladophora spp., *Chaetomorpha linum, Bryopsis plumosa*	Jensen 1975
	Cladophora spp., *Chaetomorpha linum,* **Laboratory**: *Bryopsis plumosa*	Jensen 1980a after Gascoigne 1956 and after Jensen 1975
Limapontia senestra	*Cladophora rupestris*	Graham 1955 after Gascoigne 1952 and after Gascoigne 1954
	Cladophora	Gascoigne & Sartory 1974
	Cladophora rupestris	Jensen 1980a after Gascoigne 1956
Limapontia depressa	*Vaucheria, Rhizoclonium, Conferva*	Graham 1955 after Gascoigne 1954
	Vaucheria spp., *Rhizoclonium riparium*	Jensen 1980a after Gascoigne 1956 and after Hartog 1959
	Laboratory: *Chaetomorpha*	Jensen 1994
	Vaucheria	Gascoigne & Sartory 1974
Olea hansineensis	Opisthobranchia-eggs	Jensen 1999 after Haefelfinger 1962
	Eggs of *Haminoea virescens, Aglaja diomedea, Gastropteron pacificum,* **Laboratory**: Eggs of *Archidoris montereyensis, Hermissenda crassicornis, Dendronotus iris*	Crane 1971
Placida aoteana	*Codium fragile, Codium convolutum, Bryopsis vestita*	Trowbridge 2004 after Trowbridge 1998b, after Willan & Morton 1984, after Burn 1989
Placida capensis	specimens of Codiaceae	Macnae 1954
Placida daguilarensis	*Bryopsis* sp., *Derbesia* sp.	Jensen 1990b
Placida dendritica	*Bryopsis plumosa*	Brüel 1904
	Ulva	Brüel 1904 after Trinchese 1876b
	Codium tomentosum	Brüel 1904 after Hecht 1895
	Codium tomentosum, Bryopsis	Graham 1955 after Gascoigne 1954
	Hermaea paucicirra	Marcus, E. DuB.-R. 1972 after Salvat 1968
	Codium tomentosum	Clark 1975
	Codium sp., *Bryopsis plumosa*	Jensen 1980a after Fretter 1941 and after Greene 1970
	Bryopsis	Bleakney 1989 after Thompson 1976 and after Millen 1980
	Bryopsis plumosa	Marzo, di et al. 1993
	Codium adhaerens, Codium tomentosum, Codium vermilara, Bryopsis plumosa, Bryopsis hypnoides, (introduced) *Codium fragile*	Trowbridge 2004 after Alder & Hancock 1843 and after Thompson 1976
	Codium spp., *Bryopsis plumosa, Bryopsis corticulans*	Williams & Walker 1999 after Jensen 1980 and Trowbridge 1991a, 1992, 1995
Placida kingstoni	*Bryopsis* sp.	Jensen 1980a
	Bryopsis plumosa, Cladophora	Jensen 1981
Placida viridis	*Bryopsis plumosa*	Jensen 1980a after Schmekel 1968 and after Monselise & Mienis 1977
Placida sp. (Behrens 2004)	*Codium magnum*	Behrens 2004
Stiliger fuscovittatus	*Polysiphonia pacifica*	Jensen 1980a after Lance 1962
Stiliger vesiculosus	eggs of *Favorinus branchialis*	Jensen 1980a after Haefelfinger 1962

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Biogeography of the Sacoglossa (Mollusca, Opisthobranchia)*

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Abstract. The Sacoglossa (Mollusca, Opisthobranchia) comprise almost 400 nominal species level taxa. Of these 284 are considered valid (i.e., no published synonymies) in this study. About half of the nominal species have been described before 1950, and the 10 most productive taxonomists have described about half of the species. Distributions of all valid species are reviewed. The highest diversity is found in the islands of the Central Pacific, though species diversity is almost as high in the Indo-Malayan sub-province. The Caribbean forms another center of species diversity. These three areas are distinguished by the high number of Plakobranchoidea. Similarity among provinces is generally low. Endemicity is high in most provinces, but this may be an artifact of collecting activity. The decrease in number of species with latitude is spectacular, and the number of cold-water endemics is very low, indicating that sacoglossans in cold temperate regions are mostly eurythermic warm water/ tropical species. The highest number of species in cold temperate areas is found in Japan and Southeastern Australia. This coincides with high species diversity of the algal genus *Caulerpa*, which constitutes the diet of all shelled and many non-shelled sacoglossans.

Keywords. Species diversity, endemism.

1. INTRODUCTION

Information on biogeography is important for understanding speciation and phylogeny as well as for making decisions about conservation. Ideally, combining a phylogenetic tree with a distributional map should give information on whether species dispersed from a center of origin or were the result of vicariance events. For most marine invertebrate groups, however, phylogenies are not fully resolved and/or taxonomy is not yet stable, and even information on distributions is incomplete. Species are still being split or synonymized, and new and undescribed species are discovered. In a worst case scenario a distribution map would show the activities of taxonomists rather than actual species distributions. In the present study existing distributional data for the Sacoglossa (Mollusca: Opisthobranchia) is reviewed and analyzed with regard to different biogeographic theories as well as activities of taxonomists over time. Phylogenetic analysis has been performed at the genus level (Jensen 1996a), and for one genus, *Thuridilla*, at species level (Gosliner 1995). The relationship of the Sacoglossa to other opisthobranchs has been discussed in several recent publications (Jensen 1996b; Mikkelsen 1996, 1998; Tholleson 1999; Wägele et al. 2003).

Sacoglossans are suctorial herbivores; only two or three species are oophagous, feeding on the eggs of other opisthobranchs (Jensen 1993a, 1997a). This means that they have depth distributions restricted to the photic zone, i.e. generally <100m. Sacoglossans are also dietary specialists, the majority of species feeding on siphonaceous green algae, especially *Caulerpa* spp. (Jensen 1997a). Hence they only occur in the habitats where these algae are found. The total number of valid species is around 300, but new species are still described and other species are synonymized.

2. MATERIALS AND METHODS

Distributional data for all species of Sacoglossa were taken from the literature. The study has included most publications of original descriptions to get the type localities. However, in the case of the oldest descriptions, the publications by Schmekel & Portmann (1982) and Bouchet (1984) have been used. Also, national and regional faunal checklists have been included, as well as records published on the Sea Slug Forum (http://www.-seaslugforum.net/). All nominal species listed in Appendix 1 have been included in the first analysis for bias of taxonomic expertise and scientific activity. In the distributional analyses, however, only species considered valid in this study have been included. As the present study is not a taxonomic analysis, species identifications and synonymizations, with a few controversial exceptions, will not be discussed. Only synonymies that have been published and not subsequently contested are used. Thus species that have only been mentioned once in the literature are, with few exceptions mentioned in the text, considered valid.

Biogeographic regions and provinces were taken from BRIGGS (1995) (Fig. 1), and sacoglossan distributions among these provinces were recorded. Although it must be assumed that a species occurs continuously between the extreme points of distribution, species were only scored as occurring in a region or province if at least one published record existed. The number of endemic species was determined for each province. As some regions were clearly underrepresented with regards to faunistic studies on opisthobranchs, a few regions have been merged or deleted from the analyses. Similarity between biogeographic regions or provinces was analyzed using three indices: CJ= Jaccard's coefficient= 100(a/(N1+N2-a)) (Valentine 1966), SD= Dice coefficient = 100(2a/(2a+b+c)) (LEAL & BOUCHET 1991), and I=index of inclusion= 100(a/Nmin) (GOLIKOV 1989). These indices differ in the weight placed on shared species (a) compared to total number of species in the compared regions (N1, N2), and species found exclusively in one or the other of the compared regions (b, c).

3. RESULTS

3.1. Fossil history

After the description of live specimens of bivalved sacoglossan gastropods (KAWAGUTI & BABA 1959), several papers on fossil species of these sacoglossans appeared. The first reviews of fossil sacoglossans were those of BOETTGER (1963) and KAY (1968). There have been extensive discussions about the identity of the Recent *Tamanovalva*, *Edenttellina* and *Midorigai* and the Middle Eocene genus *Berthelinia* (e.g. EDMUNDS 1963; BURN 1998). KEEN & SMITH (1961) listed several other fossil species and included all in the family Juliidae Dall, 1898, which had previously been located in the Bivalvia. More

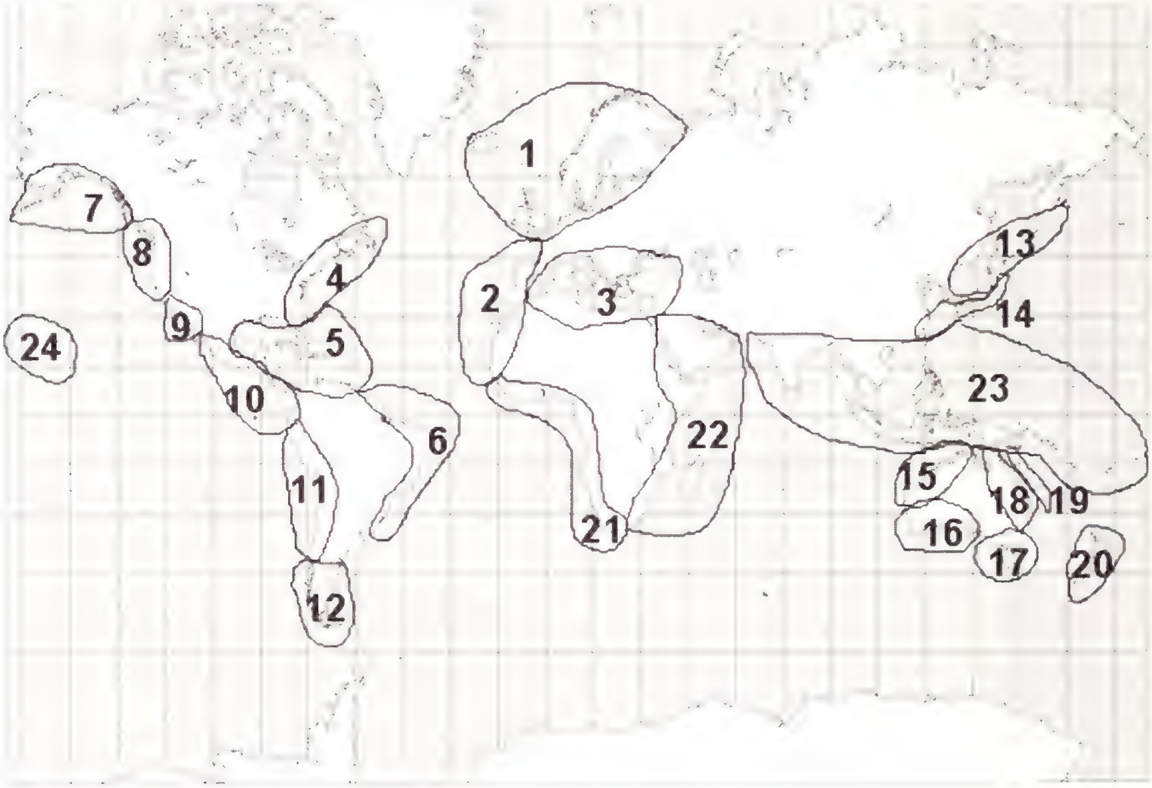

Fig. 1. Map showing biogeographic regions used in the present study. Regions have been modified from BRIGGS (1995). **1.** Northeast Atlantic. **2.** Lusitanian. **3.** Mediterranean (including the Black Sea). **4.** Northwest Atlantic. **5.** Caribbean. **6.** Southwestern Atlantic tropical and warm temperate. **7.** Aleutian. **8.** Oregonian. **9.** Californian. **10.** Mexican-Panamanian. **11.** Southeastern Pacific warm temperate. **12.** Cold temperate South America. **13.** Northwest Pacific cold temperate. **14.** Northwest Pacific warm temperate. **15.** Northern and northwestern Australia. **16.** Southwestern and southern Australia. **17.** Southeastern Australia. **18.** Northeastern Australia. **19.** Great Barrier Reef. **20.** New Zealand. **21.** Southeast Atlantic. **22.** Western Indian Ocean. **23.** Indo-Polynesian region (including Ryukyu Islands). **24.** Hawaii.

recently several more fossil bivalved sacoglossans have been described (see LE RENARD et al. 1996 for review), and also a single species of *Volvatella* has been described from the Lower Miocene of France (VALDÉS & LOZOUET 2000). Thus there may be two or five Recent genera of bivalved sacoglossans, whereas there are 9 fossil genera extending from the Lower Eocene to Lower Pliocene. Most fossil species have been found in European localities, but a few are from the Caribbean, and one each from Australia and Indonesia. However, no doubt more fossil species will be described in the future.

The temporal and spatial distribution of fossil sacoglossans indicates that they arose as part of the Tethys Sea fauna. As sea level receded and temperatures cooled down, their distribution became more restricted, and today there is only one species of *Berthelinia* in the Caribbean and one in the Panamanian region; the remaining species are Indo-West Pacific. *Julia* has one species in the East Pacific; the remaining species are Indo-West Pacific. For *Volvatella* there is only one species in the Caribbean, one in warm temperate South Africa, and the remaining species are Indo-West Pacific. The disappearance of a major part of the coral reefs at the end of the Cretaceous (BRIGGS 1995) may have created ideal conditions for speciation of siphonaceous green algae when sea level rose again in early Eocene.

3.2. Recent species

Slightly more than half (199 of 387) of the nominal species have been described before 1950. There is a distinct peak around the 1860s and 1870s when PEASE and BERGH were most active describing species from the Indo-West Pacific and Costa and Trinchese worked in the Mediterranean (Fig. 2). After 1950, it is especially the MARCUSes (39 species) and K. BABA (30 species) who dominate the number of new species (Table 1). The 10 most productive authors or groups of authors have described almost 50 % of the species.

Of the 387 nominal species 284 (73%) have been included in the similarity analyses. The number of species recorded from regions and provinces shown in Fig. 1 is listed in Table 2. Some regions are distinctly underrepresented in regards to number of records. This is true for most of the southern cold temperate zone, but also for tropical East Atlantic and southern East Pacific. Most of the biogeographic regions and provinces are supported by the present study as indicated by the percentage of endemic species. The regions and provinces with less than 10% endemism will be discussed below.

The Northeast Atlantic and Mediterranean were the earliest studied areas. The number of species described dur-

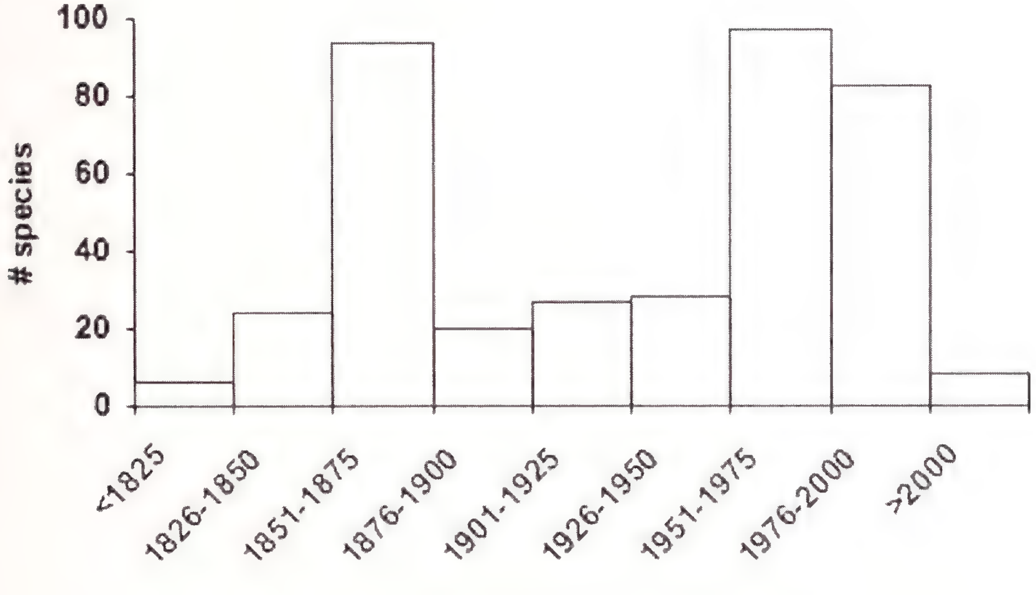

Fig. 2. Frequency of species descriptions through time.

ing the 19th century is high, but many species have subsequently been synonymized. New species are still discovered (Ortea & Templado 1990; Perrone 1990; Cervera et al. 1991), old synonyms resurrected (Cervera & Lopez-González 1996; Ortea & Moro 1998), and the validity of some species, even some of the more recently described ones, is still debated (Cervera et al. 2006). In addition, species ranges appear to be expanding (Thompson 1983; Ortea et al. 1997; Evertsen & Bakken 2002). Hence the present analyses represent an *ad hoc* picture of species distributions and diversity.

Three faunal provinces are recognized in the Northeast Atlantic: the warm temperate Mediterranean Sea, including the Black and Azov Seas (no sacoglossans occur in the Caspian and Aral Seas), the warm temperate Lusitanian province and the cold temperate Northeast Atlantic Boreal region (Briggs 1995). Three species appear to be endemic to the Northeast Atlantic cold-water region. However, two of these may be identical to Lusitanian and/or Mediterranean species. The possible synonymy of *Ercolania nigra* and *E. viridis* is currently under study by the present author, and it is also likely that *Calliopaea oopha-*

Table 1. Number of species described by different authors (called "group(s)", when with one or several co-authors) through time. All nominal taxa have been included.

Author	# species described
Marcus (& Marcus), 1955–1982	39
Baba (et al.), 1935–1959	30
Jensen (et al.), 1980–1999	23
Bergh, 1871–1905	20
Pease, 1860–1871	17
Ortea (et al.), 1981–2006	15
Trinchese, 1869–1895	14
Ichikawa, 1993	11
Thompson (et al.), 1973–1988	10
A. Costa, 1862-1876	10
Total for 10 authors (groups)	189
Total # nominal species	387
Percentage described by 10 most productive authors (groups)	49
Total # authors (groups)	104
Average # species per author (group)	3.7

Table 2. Species distribution and endemicity of sacoglossan opisthobranch in biogeographic regions as defined by Briggs (1995). Only species considered valid in the present study have been included. n.d. not determined.

Region	# Species	# endemics (%)
1. Northeast Atlantic boreal	11	3* (27)
2. Lusitanian	40	5 (12.5)
3. Mediterranean + Black Sea	37	8 (22)
4. Northwest Atlantic boreal	6	1 (17)
5. Caribbean incl. Florida	49	21 (43)
6. Southwestern Atlantic tropical + warm temperate	19	3 (16)
7. Aleutian	6	0
8. Oregonian	8	0
9. Californian	9	0
10. Mexican-Panamanian	23	9 (39)
11. Southeast Pacific warm temperate	6	0
12. Cold temperate South America	4	2 (50)
13. Northwest Pacific cold temperate	29	5 (17)
14. Northwest Pacific warm temperate	41	9 (21)
15. North and Northwestern Australia	23	4 (17)
16. South and Southwestern Australia	22	6 (27)
17. Southeastern Australia	15	6 (40)
18. Northeastern Australia	18	1 (5.5)
19. Great Barrier Reef	22	0
20. New Zealand	5	1 (20)
21. Southeastern Atlantic	9	4 (44)
22. Western Indian Ocean + Red Sea	32	8 (25)
23. Indo-Polynesian, incl. Ryukyu Islands	107	n.d.
24. Hawaii	25	6 (24)

*Two of these species may be synonymous with Lusitanian and Mediterranean species.

Table 3. Similarity between provinces of the Atlantic Ocean. The Southeast Atlantic is excluded due to lack of information. In this and all following tables only species considered valid in the present study have been included. CJ Jaccard's Coefficient; SD Dice Coefficient; I Index of inclusion; N number of species included; n.d. not determined.

a.

CJ \ SD	**NE Atl cold N=11**	**NW Atl cold N=6**	**Lusitan. N=40**	**Medit N=38**	**Carib N=49**	**Brazil N=19**
NE Atl cold	-	23.5	27.5	28.6	3.33	n.d
NW Atl cold	13.3	-	8.70	9.09	14.5	n.d.
Lusitanian	15.9	4.55	-	66.7	31.5	13.6
Mediterranean	16.7	4.76	50.0	-	23.0	n.d.
Caribbean	1.69	7.84	18.7	13.0	-	47.1
Brazil	n.d.	n.d.	7.27	n.d.	30.8	-

b.

I	**NE Atl cold**	**NW Atl cold**	**Lusitanian**	**Medit**	**Carib**
NE Atl cold	-	-	-	-	-
NW Atl cold	33.3	-	-	-	-
Lusitanian	63.6	33.3	-	-	-
Mediterranean	63.6	33.3	68.4	-	-
Caribbean	9.09	66.7	35.0	26.3	-
Brazil	n.d.	n.d.	21.1	n.d.	84.2

ga Lemche, 1974 is a subtidal variety of *C. bellula* d'Orbigny, 1837. *Limapontia depressa* may be the only endemic from this cold-water region, and even that species may occasionally be found further south on the French Atlantic coast (M. Poddubetskaia, Bordeaux, pers. comm. 2006). The other two species of *Limapontia* only extend into the Lusitanian and/or Mediterranean province (Pruvot-Fol 1954; Schmekel & Portmann 1982); *L. capitata* occurs in all three provinces and *L. senestra* occurs in two provinces. *L. capitata* is also the only sacoglossan recorded from Iceland and the Faroe Islands (Platts 1985). Hence the genus *Limapontia* is probably a cold-water, eurythermal genus, which is endemic to the Northeast Atlantic-Mediterranean region. Various records exist of unidentified species of *Limapontia* from other regions (e.g. Engel et al. 1940; Burn 1973; Schrödl 1996). However, these need confirmation as many species of *Ercolania* lack cerata in juveniles.

One species, *Hermaea variopicta*, has its northern limit along the south coast of the UK (Lemche & Thompson 1974). Two species, *Elysia viridis* and *Calliopaea bellula*, have their northern limit around Trondheimfjord (Brattegard & Holthe 2001). Four species, *Alderia modesta, Placida dendritica, Limapontia capitata* and *L. senestra*, occur in the northernmost part of Norway (Vader 1981; Brattegard & Holthe 2001; Evertsen & Bakken 2002; pers. obs.), and all three species of *Limapontia* plus *Alderia modesta* have been recorded from the White Sea (Roginskaya 2000; Martynov et al. 2006). Prior to 1997 *P. dendritica* had not been recorded from Norway north of the Bergen area (Evertsen & Bakken 2002).

Five species appear to be endemic to the Lusitanian province. These have all been described after 1980, so it is possible that they will be found in neighboring regions in the future. The Canary Islands has the highest species diversity of this region (27 of 40 species have been recorded here). A number of Caribbean species have been recorded from these islands in recent years (Ortea et al. 1998). Since the sacoglossan fauna of these islands has been well documented over many years (Ortea 1981; Fernandez-Ovies & Ortea 1986; Cervera et al. 1988; Ortea et al. 1990; Templado et al. 1990), and only one or a few specimens have been collected at one single time far from their native distribution area, these species have most likely been transported by human activities (Chapman & Carlton 1991). Few species have been recorded from Madeira, Salvage, Cape Verde and Azores Islands (Ortea 1981; Ortea & Templado 1990; Ortea et al. 1988, 1990, 1998; Malaquias & Calado 1997; Jensen 1995, in prep.). There is an old record of the shelled *Ascobulla fragilis* from the Atlantic coast of Spain, which is cited in more recent publications (Pilsbry 1895; Pruvot-Fol 1954; Cervera et al. 2006). As this species feeds exclusively on *Caulerpa*, which does not extend this far north (Doumenge 1995), this needs to be re-examined.

Eight species are endemic to the Mediterranean. Some of these may be synonyms of other species with wider distributions (SCHMEKEL & PORTMANN 1982; THOMPSON 1988). Eight amphi-Atlantic (one of which may be cosmopolitan), eight Northeast Atlantic-Lusitanian, and five endemic species do not extend into the eastern basin of the Mediterranean. Only four species found in the eastern basin of the Mediterrnanean do not occur in the western basin; two of these have been described recently (THOMPSON 1988). The total number of sacoglossans in the eastern basin is only 17 whereas 34 species are known from the western basin (SWENNEN 1961; BARASH & DANIN 1971; SCHMEKEL & PORTMANN 1982; THOMPSON 1983; BOUCHET 1984; THOMPSON et al. 1985; THOMPSON 1988; THOMPSON & JAKLIN 1988; CATTANEO-VIETTI & THOMPSON 1989; CERVERA et al. 2006). The southern coast of the Mediterranean has been insufficiently studied. It is uncertain whether two or three species extend into the Black and Azov Seas. *Limapontia capitata* and *Calliopaea bellula* (as *Stiliger bellulus*) have been recorded previously (MURINA & ARTEMJEVA 1997), but recent pictures on the Sea Slug Forum (KURAKIN 2002) have shown that *Ercolania viridis* is present, and it remains to be seen whether the species previously identified as *C. bellula* has been misidentified, or whether both species occur.

The Lusitanian and Mediterranean provinces have very high similarity indices (Table 3). The combined number of species amounts to 52, which is very close to the species diversity found in the Caribbean. However, the number of Plakobranchidae is lower in the eastern Atlantic provinces (Table 9).

BRIGGS (1995) recognizes one circumpolar Arctic region comprising Spitzbergen, Greenland and the northern coasts of North America and Russia. No sacoglossans have been recorded from Spitzbergen (GULLIKSEN et al. 1999) or the north coast of North America (BLEAKNEY 1996; GODDARD & FOSTER 2002). The four species occurring in the White Sea also occur in the Russian part of the Barents Sea (ROGINSKAYA 2000; MARTYNOV et al. 2006). In addition, MARTYNOV et al. (2006) mentions an old record of a single juvenile specimen of *Placida dendritica* from Kola Bay. This indicates that this area is influenced by the North Atlantic Current and should be included in the boreal region. The single specimen of *Alderia modesta* recorded from western Greenland (PLATTS 1985) could be attributed to larvae transported from Canada, which may occasionally be able to find suitable habitats for metamorphosis in Greenland. The latitude of Disko Fjord is about the same as northern Norway, where the species occurs regularly. It should be mentioned that in Danish waters this species seems to have disappeared from localities where prior to 1997 it was abundant (pers. obs.). Whether this is due to habitat deterioration or increased temperature is unknown.

The fauna of the Northwest Atlantic is also very well studied (e.g. MARCUS & MARCUS 1970; MARCUS 1972a,b; MARCUS & HUGHES 1974; CLARK 1975; JENSEN & CLARK 1983; BLEAKNEY 1996), though new species are still being described from the tropical waters (ORTEA & ESPINOSA 1996, 2000, 2001, 2002; CABALLER et al. 2006; PIERCE et al. 2006). Only 6 species occur in the cold temperate province; one of these, *Placida dendritica*, may be cosmopolitan (BLEAKNEY 1989) and one, *Alderia modesta*, is circum-boreal. Apparently only one species, *Elysia catulus*, is endemic to the Northwest Atlantic cold water region (CLARK 1975). This species feeds on the seagrass *Zostera marina*, which does not occur in Florida. It is possible that *E. catulus* is a dark pigmented variety of the other seagrass feeding species, *Elysia serca* (JENSEN 1982), in which case there will be no endemic species for the Northwest Atlantic. *Ercolania fuscata* may occur from Nova Scotia, Canada to Sao Paolo, Brazil, but this distribution is based on synonymization with *E. vanellus* and *E. talis* (JENSEN & CLARK 1983). Two species, *Elysia chlorotica* and *Hermaea cruciata*, have their southern limit in Florida (JENSEN & CLARK 1983), i.e., just south of the cold-water region. The former species also occurs in the northern part of the Gulf of Mexico (BOONE 1982), and the latter has its northern limit in Massachusetts (MARCUS 1972a). The species presently known as *Limapontia zonata*, and known only from its original collection (GOULD & BINNEY 1870), is probably a flatworm; no sacoglossan has transverse pigment bands.

A separate Carolinian province could not be distinguished for sacoglossan opisthobranchs, and no difference is evident between the continental and insular parts of the Caribbean (CLARK & DEFREESE 1987), including Bermuda (CLARK 1984), although these provinces were considered distinct by BRIGGS (1995). However, the majority of studies involving sacoglossans are from the Caribbean islands. The limit between cold-water and tropical faunas appears to be along the coast of Florida (JENSEN & CLARK 1983); 36 of the 49 Caribbean species have been recorded from Florida (THOMPSON 1977; MARCUS 1977, 1980; CLARK 1982; CLARK & DEFREESE 1987; PIERCE et al. 2006; VALDÉS et al. 2006). The degree of endemism in the Caribbean is exceptionally high (Table 2). Especially the number of Plakobranchidae is high (Table 9), indicating that speciation in this family has taken place within the province. Five of the 21 endemic species have been described after 1990, so they may be found outside this province in the future or be synonymized with other species. As for the Mediteranean and Lusitanian provinces, synonymies are extensively debated and the status of several species remains uncertain (JENSEN & CLARK 1983; MARCUS 1980; VALDÉS et al. 2006).

Table 4. Similarity of provinces of East Pacific. Due to the high similarity between Aleutian, Oregonian and Californian provinces, these have been merged (Al+Or+Cal). Other abbreviations as in Table 3.

a.

CJ \ SD	**Aleutian N=6**	**Oregonian N=8**	**Californian N=9**	**Al+Or+Cal N=10**	**Mex-Panam N=23**	**SE Pacific N=9**
Aleutian	-	85.7	66.7	-	27.6	n.d.
Oregonian	75.0	-	82.4	-	38.7	n.d.
Californian	50.0	70.0	-	-	50.0	n.d.
Al+Or+Cal	-	-	-	-	48.5	10.5
Mex-Panam	16.0	24.0	33.3	32.0	-	43.8
SE Pacific	n.d.	n.d.	n.d.	5.56	28.0	-

b.

I	**Aleutian**	**Oregonian**	**Californian**	**Al+Or+Cal**	**Mex-Panam**
Aleutian	-	-	-	-	-
Oregonian	100.0	-	-	-	-
Californian	83.3	87.5	-	-	-
Mex-Panam	66.7	75.0	88.9	80.0	-
SE Pacific	n.d.	n.d.	n.d.	11.1	77.8

The genus *Bosellia* appears to be an Atlantic warm-water genus with one amphi-Atlantic, one Canary Islands endemic (Fernandez-Ovies & Ortea 1986), and two Caribbean species (Marcus 1973). There are some scattered reports of *Bosellia* from the Indo-Pacific region (Marcus 1978; Imamoto 2004; Pittman 2004; Riek 2006). However, too few specimens have been recorded to either identify them as one of the described species or decide that they are undescribed species.

Briggs (1995) recognized a tropical Brazilian province extending to just south of Rio de Janeiro. For sacoglossans, most Brazilian species extend south to the area around Sao Paolo (Marcus (Er.) 1955, 1957; Marcus & Marcus 1967; Marcus (Ev.) 1977). This can probably be explained by the extensive collecting activity of the Marcuses around Sao Paolo; 47% of the Brazilian species have been described by them. Furthermore, more than 90% of the Brazilian species also occur in the Caribbean (Table 3b), and the number of endemic species is low (Table 2). This is most likely also due to the activities of the Marcuses in both these regions.

Trowbridge (2002) reviewed the Northeast Pacific sacoglossan fauna. She recognized four provinces, but unfortunately the borders are not exactly the same as suggested by Briggs (1995). This is especially evident for the Californian province, in which Trowbridge records one species of the bivalved genus *Berthelinia* plus a couple of unidentified/ undescribed species. The present study found no endemic species in the Aleutian, Oregonian and California provinces and hence these were merged. Also, no difference was obvious between the Mexican and Panamanian provinces, which have also been merged before comparisons with other provinces (Table 4). In the Mexican-Panamanian province four species have been recorded after the publication of Trowbridge's paper (Behrens & Hermosillo 2005; Krug et al. 2007) and one species, *Ascobulla californica* (originally described as *Cylindrobulla californica* by Hamatani (1971)), was not considered a sacoglossan by Trowbridge (2002). The occurrence of *Alderia modesta* in the Mexican-Panamanian region is probably the recently described species, *Alderia willowi* (Krug et al. 2007), which occurs southwards from central California. The monotypic genus *Olea* is endemic to the Northeastern Pacific region, extending from the Aleutian to the Californian province (Trowbridge 2002). *Hermaea vancouverensis* is a cold-water species, extending across the Bering Strait to the Kurile province (Chernyshev 2005). One species, *Elysia hedgpethi*, occurs from British Columbia, Canada to Chile (Schrödl 1996; Trowbridge 2002), though the occurrence in Chile needs verification.

The species extending into the warm temperate region of the Southeast Pacific almost all are shared with the tropical Mexican-Panamanian region (Schrödl 1996; Trowbridge 2002; Behrens & Hermosillo 2005). *Julia thecaphora* is considered the oldest name for *J. equatorialis*, which was also described from the tropical East Pacific. Only four species have been recorded from cold-temperate South America, one from the Atlantic coast and three from the Pacific (Marcus 1959; Schrödl 1996; Munian & Ortea 1997). Due to the low number of species and sparse collecting activity, the species from the Southeast Pacific coast have been considered as one province for analyses.

Table 5. Similarity of Japanese biogeographic provinces and of Northwest and Northeast Pacific provinces. The Japanese provinces have also been compared to the neighboring Central Pacific sub-province. Abbreviations: see Table 3.

a.

CJ \ SD	**Japan cold temp., N=26**	**Japan warm temp., N=41**	**Ryukyu N=33**	**Central Pacif. N=51**	**NW Pacif. cold temp., N=29**	**NE Pacif. cold temp. N=10**
Japanese cold temp.	-	59.7	27.1	26.0	-	n.d.
Japanese warm temp.	42.6	-	37.8	37.0	n.d.	n.d.
Ryukyu	15.7	23.3	-	38.1	n.d.	n.d.
Central Pacific	14.9	22.7	23.5	-	n.d.	n.d.
NW Pacific cold temp.	-	n.d.	n.d.	n.d.	-	20.5
NE Pacific cold temp.	n.d.	n.d.	n.d.	n.d.	11.4	-

b.

I	**Japan cold temp.**	**Japan warm temp.**	**Ryukyu**	**NW Pacif. cold temp.**
Japanese cold temp.	-	-	-	-
Japanese warm temp.	76.9	-	-	-
Ryukyu	30.8	42.4	-	-
Central Pacific	38.5	41.5	48.5	-
NE Pacific cold temp	-	n.d.	n.d.	40.0

Four biogeographic regions or provinces can be distinguished along the coasts of Japan. Biogeographically the southernmost archipelago of Ryukyu belongs in the vast tropical Indo-Polynesian province (Briggs 1995), but being under Japanese jurisdiction, the sacoglossan fauna has been studied mostly by Japanese scientists (e.g. Baba 1936; Hamatani 1980; Ichikawa 1993). Hence Ryukyu has been included in both analyses of the Japanese fauna (Table 5) and of the Indo-West Pacific one (Table 7). The warm-water temperate region comprises southern and eastern Japan, including the well studied Seto Inland Sea and Sagami Bay. The corresponding continental coast of China has been insufficiently studied, and only 14 species have been recorded from southern Korea (Koh 2002a,b, 2003, 2005a,b,c; Rudman, Sydney, pers. comm. 2007). The cold-water temperate oriental province includes the central and western coasts of Honshu, whereas the northernmost island of Hokkaido belongs to the Kurile province (Briggs 1995). The cold-temperate fauna of Japan contains more species (N=26) than any other cold-water fauna. A few shelled species extend into this province, which is also seen in southern Australia, but not in other cold-water provinces. Only three additional sacoglossan species have been recorded from the Kurile province (Baba 1935; Chernyshev & Chaban 2005; Trowbridge 2006) and these were only included in the comparison of Northeast and Northwest Pacific cold-water faunas (Table 5). The highest number of species has been recorded from the warm temperate region (e.g. Baba 1949, 1952a,b, 1955, 1957, 1959, 1966; 1968; Hamatani 1968, 1969, 1972, 1976a,b, 1994; Kawaguti & Baba 1959; Hirano et al. 2006); in fact Baba described 59% of the species from this province and 69% of the species from the cold-water region of Japan. A few of the species described by Baba have been synonymized with more widespread Indo-West Pacific species (Baba 1974; Jensen 1985). On the other hand, many of Baba's species have been identified outside Japan (Jensen 1985; Carlson & Hoff 1978, 2003; Burn 1998, 2006).

The Northeast Australian and Great Barrier Reef faunas (Burn 1966b; Thompson 1973; Marshall & Willan 1999; Wägele & Johnson 2001) are so closely related to each other that no endemics have been recorded from the Great Barrier Reef and only one endemic species, *Placida fralila*, has been recorded from Northeast Australia (Table 2). Hence these two provinces were merged for similarity analyses, and the combined province has two endemic species (*Elysia bennettae, P. fralila*). For the Great Barrier Reef 30% of the species were listed as unidentified and/or undescribed (Marshall & Willan 1999). This part of Australia has been included in the Indo-Polynesian province by Briggs (1995). This is supported by the low endemicity, and also, the similarity with the fauna of the South Pacific islands is higher than with any of the other Australian provinces (Tables 6 and 7). The North and Northwestern Australian fauna has rather high similarity to the Western Indian Ocean fauna (Table 7). This is in spite of the fact that almost 40% of the species have been described by the present author within the last 20 years (Jensen 1993b, 1997b,c; Jensen & Wells 1990). The fauna of the South and Southwestern Australia has

Table 6. Similarity of provinces of the Australian continent. Due to the high similarity between the Northeast Australian province and the Great Barrier Reef, these two provinces have been merged (NE Aus+GBR). Abbreviations as in Tab. 3.

a.

CJ \ SD	**NE Austr N=18**	**GBR N=22**	**NE Aus+ GBR N=28**	**N+NW Austr N=23**	**SW+S Austr N=22**	**SE Austr N=15**
NE Australia	-	60.0	-	34.1	30.0	30.3
GBR	42.9	-	-	26.7	18.2	16.2
NE Aus+GBR	-	-	-	31.4	28.0	27.9
N+NW Austr	20.6	15.4	19.0	-	48.8	26.3
SW+S Austr	17.6	10.0	16.3	32.4	-	43.2
SE Austr	17.9	8.82	16.2	15.2	27.6	-

b.

I	**NE Austr**	**GBR**	**NE Aus+GBR**	**N+NW Austr**	**SW+S Austr**
NE Australia	-	-	-	-	-
GBR	66.7	-	-	-	-
NE Aus+GBR	-	-	-	-	-
N+NW Austr	38.9	27.3	34.8	-	-
SW+S Austr	33.3	18.2	31.8	50.0	-
SE Austr	33.3	20.0	40.0	33.3	53.3

the highest affinity to the fauna of North and Northwestern Australia, and the other way around, whereas the fauna of Southeastern Australia (Burn 1958, 1960, 1965, 1974, 1998, 2006) has a higher affinity to the fauna of South and Southwestern Australia than to that of Northeastern Australia and the Great Barrier Reef (Table 6). This may change when the 50% unidentified/undescribed species listed for Southeastern Australia (Burn 2006) are properly named.

Very few sacoglossans have been recorded from New Zealand (Powell 1937; Willan & Morton 1984; Trowbridge 1995a; Spencer & Willan 1995). The fauna consists of widespread species and one endemic (Table 2). Hence this fauna has not been further analyzed in the present study.

The sacoglossan fauna of the Red Sea (Eliot 1908; O'-Donoghue 1929; Heller & Thompson 1983) has about the same affinity to the fauna of the Indian subcontinent as to the Western Indian Ocean, and the index of inclusiveness (I) for the Red Sea and India *sensu lato (s.l.*, see below) is twice that for the Red Sea and the Western Indian Ocean (Table 7b). Also, two out of the ten recorded species are endemic to the Red Sea. Hence the Red Sea should be considered a separate province. In other groups of invertebrates Lessepsian migrants are common. For sacoglossans this appears to be a small and recent problem (Yokes 2001, 2002; Rudman 2002). Except for these few species, the Red Sea does not share any species with the Mediterranean.

The sacoglossans found in southwestern Africa are more closely related to those found in southeastern Africa than to any other region or province (Gosliner 1987a); in fact no species are shared with the Brazilian fauna and only one species, *Placida dendritica*, is shared with the Lusitanian province. Hence this province has been considered in connection with the Western Indian Ocean province. Endemicity is high, but this could be due to the poor knowledge of tropical western Africa. Only one species has been described from this region (Marcus & Marcus 1966), so this was not included in the present study. The East Atlantic species *Elysia viridis* apparently occurs from central Norway (Brattegard & Holthe 2001) to South Africa (Gosliner 1987a), though no records exist between the Senegal (Pruvot-Fol 1953) and South Africa, and Gosliner (1998) has subsequently changed the identification to *Elysia* sp. The species was originally identified in South Africa as the Indian species *E. punctata* by MacNae (1954). Gosliner (1987a) found a distinct faunal separation for opisthobranchs at Port Elizabeth, whereas Briggs (1995) considers the coast between the Cape of Good Hope and north of Durban one province. In the present study Port Elizabeth has been used to separate the faunas of southwestern Africa and the Western Indian Ocean.

The Western Indian Ocean is considered a separate province by Briggs (1995). The sacoglossan fauna of this province has a high similarity with the South Pacific and North and Northwestern Australia (Table 7). The affinity with the fauna of India *s.l.* (India, Sri Lanka and Maldives) is considerably lower, and also the affinity with the Indo-

Table 7. Similarity of provinces of the Australian continent. Due to the high similarity between the Northeast Australian province and the Great Barrier Reef, these two provinces have been merged (NE Aus+GBR). Abbreviations as in Tab. 3.

a.

CJ \ SD	**SW Afr. N=8**	**WIO N=27**	**Red Sea N=10**	**India *s. l.* N=20**	**Indo-Malay N=48**	**N+NW Austr N=23**	**Centr. Pac. isl. N=51**	**NE Aus + GBR N=28**	**S Pacific N=33**	**Hawaii N=25**	**Ryukyu N=33**
SW Afr.	-	28.6	11.1	7.14	n.d.	12.9	n.d.	n.d.	9.76	n.d.	n.d.
WIO	16.7	-	27.0	17.0	24.0	32.0	35.9	25.5	36.7	n.d.	n.d.
Red Sea	5.88	15.6	-	26.7	n.d.	18.2	n.d.	n.d.	18.6	n.d.	n.d.
India *s. l.*	3.70	9.30	15.4	- 20.6	14.0	19.7	12.5	22.6	17.8	7.55	
Indo-Malay	n.d.	13.6	n.d.	11.5	-	22.5	50.5	28.9	37.0	19.2	24.7
N+NW Austr	6.90	19.0	10.0	7.50	12.7	-	29.7	31.4	32.1	n.d.	n.d.
Centr. Pac. isl.	n.d.	21.9	n.d.	10.9	33.8	17.5	-	43.0	50.0	42.1	38.1
NE Aus+GBR	n.d.	14.6	n.d.	6.67	16.9	19.0	27.4	-	42.6	n.d.	n.d.
S Pacific	5.13	22.4	10.3	12.8	22.7	19.1	33.3	27.1	-	41.2	24.2
Hawaii	n.d.	n.d.	n.d.	9.76	10.6	n.d.	26.7	n.d.	26.1	-	13.8
Ryukyu	n.d.	n.d.	n.d.	3.92	14.1	n.d.	23.5	n.d.	13.8	7.41	-

b.

I	**SW Afr.**	**WIO**	**Red Sea**	**India *s. l.***	**Indo-Malay**	**N+NW Austr.**	**Centr. Pac. isl.**	**NE Aus + GBR**	**S Pacific**	**Hawai**
SW Afr.	-	-	-	- -	-	-	-	-	-	-
WIO	62.5	-	-	- -	-	-	-	-	-	-
Red Sea	12.5	50.0	-	- -	-	-	-	-	-	-
India *s. l.*	12.5	20.0	40.0	- -	-	-	-	-	-	-
Indo-Malay	n.d.	33.3	n.d.	35.0	-	-	-	-	-	-
N+NW Austr	25.0	34.9	30.0	15.0	34.8	-	-	-	-	-
Centr. Pac. isl.	n.d.	51.9	n.d.	35.0	52.1	47.8	-	-	-	-
NE Aus+GBR	n.d.	25.9	n.d.	15.0	39.3	34.8	60.7	-	-	-
S Pacific	25.0	40.7	40.0	30.0	45.5	39.1	63.6	46.4	-	-
Hawaii	n.d.	n.d.	n.d.	20.0	28.0	n.d.	64.0	n.d.	48.0	-
Ryukyu	n.d.	n.d.	n.d.	10.0	30.3	n.d.	48.5	n.d.	24.2	16.0

Malayan sub-province is lower. Endemicity is high (5 of 27 species), though two of these species have sometimes been synonymized with widespread Indo-West Pacific species (GOSLINER 1987b). The majority of species recorded from the Western Indian Ocean have been collected from the southern part of the region, i.e. South Africa (THOMPSON 1979; GOSLINER 1987a,b, 1995), Tanzania (ELIOT 1903, 1904; GOSLINER 1995), Madagascar (GOSLINER 1995) and Mauritius (BERGH 1888; GOSLINER 1995).

A total of 107 species of sacoglossans have been recorded from the vast Indo-Polynesian province. Most of these species are only distributed in part of the province and hence it was subdivided into five sub-provinces: The Indian subcontinent, including Sri Lanka and the Maldive Islands was considered one sub-province (10 endemic species); the Andaman Sea, the South China Sea, Indonesia and the Philippines form an Indo-Malayan sub-province (9 endemic species); the Mariana and Marshall Islands together with Micronesia were considered a Central Pacific sub-province (4 endemic species); Papua New Guinea, Solomon Islands, Fiji, Vanuatu, New Caledonia, Samoa and the Polynesian islands form a South Pacific province (6 endemic species); and as mentioned above the Ryukyu Islands form a separate sub-province (10 endemic species). Many of the endemic species have been described within the last 20 years, so they may actually have wider distributions.

Of the 107 species recorded from the Indo-Polynesian province only 12 have distributions from the Western Indian Ocean and/or the Red Sea to the Central and/or South Pacific islands, two species, *Elysia ornata* and *Ercolania coerulea*, are circum-tropical and one, *Placida dendritica*, may be cosmopolitan. Two of the 12 widespread Indo-West Pacific species are shelled (*Oxynoe viridis* and *Berthelinia schlumbergeri*), seven are plakobranchoids (5 species of *Thuridilla, Elysiella pusilla* and *Plakobranchus ocellatus*) and three are limapontioids *(Cyerce elegans, C. nigricans* and *Polybranchia orientalis*). The widest latitudinal distributions along the West Pacific rim are found in the four species that occur from the cold-temperate part of Japan to the cold-temperate part of Australia. Two of these species are the circum-tropical *Elysia ornata* and the questionably cosmopolitan *Placida dendritica*; the other two are *Elysia obtusa* and *Stiliger smaragdinus*. *P. dendritica* has been synonymized with a number of species described from different places in the Indo-West Pacific (Bleakney 1989), but the synonymy has been doubted (e.g. Trowbridge 1995b). Two species, *Oxynoe viridis* and *Elysiella pusilla*, extend from warm-temperate Japan to southern Australia. Two further species, *Thuridilla splendens* and *Polybranchia orientalis*, extend from warm-temperate Japan to Northeast Australia and the Great Barrier Reef. Four species, *Plakobranchus ocellatus, Thuridilla vatae, T. hoffae* and *Cyerce nigricans*, extend from the Ryukyu Islands to tropical Australia. Most of these species also have wide longitudinal distributions. *Plakobranchus ocellatus* occurs in a number of colour varieties, and it is possible that a complex of sibling species is involved (see discussion on the Sea Slug Forum: http://www.seaslugforum.net/find.cfm?id=13970) (last access 12th of August 2007).

The Indian sub-province has a high proportion of endemic species (50%). This is probably an artifact due to the activities of a few taxonomists who have worked only within this sub-province (Kelaart 1858; Nevill & Nevill 1869; Rao 1937; Rao & Rao 1963; Sarma 1975). Most of G. & H. Nevill's species have been synonymized, though not consistently with the same species. Although doubtful, they have been considered valid in the present study. The species described by Kelaart have been re-examined several times (Eliot 1906; O'Donoghue 1932) and they are still recognized as valid, mostly widespread Indo-West Pacific species. In spite of the high endemicity, India *s.l.* shows higher similarity to the Indo-Malayan, Central and South Pacific sub-provinces than to the Western Indian Ocean province (Table 7). The highest similarity is found between India *s.l.* and the Red Sea, but this is caused by the low number of species found in the Red Sea, and the high proportion of widespread Indo-West Pacific species.

The Indo-Malayan and Central Pacific sub-provinces have twice the number of species occurring in tropical Australia and the Western Indian Ocean and 50% more species than the South Pacific and Ryukyu Islands. This could be seen as evidence for being a center of origin for evolution of new species. Looking at species composition in the central Pacific islands (data from Marcus 1965; Johnson & Boucher 1983; Carlson & Hoff 2003), it seems more likely that they are "traps", where species dispersing from the Japanese warm-temperate and from tropical and possibly even warm-temperate Australia can find suitable habitats. The Central Pacific sub-province is the only one with less than 10% endemics, but many unidentified and/or undescribed species are known from this sub-province (Carlson & Hoff 2003; own obs.). Most biogeographic studies indicate that the triangle consisting of Indonesia, Malaysia and the Philippines and sometimes including Papua New Guinea has the highest number of species (Ekman 1953; Briggs 1995, 2005). Information on sacoglossan distributions in the Indo-Malayan sub-province has been collected from numerous sources (e.g. Bergh 1871, 1872, 1905; Eliot 1917; Lin 1986, 1990; Gosliner 1995; Gosliner et al. 1996; Debelius 1996; Jensen 1998a,b, 2003; Swennen et al. 2001). The number of sacoglossan species is slightly lower in this sub-province than in the islands of the Central West Pacific, i.e. Marianas, Marshall Islands and Micronesia. This may be a collecting artifact caused by the activities of Carlson and Hoff in Guam and neighboring islands; they recorded 91 species of which 48 (53%) were identified to species level (Carlson & Hoff 2003). However, the present similarity analyses also indicate that these islands constitute the center of species diversity. Species described from northern Australia, the South China Sea and southern Japan also occur in the Mariana Islands. The genus *Gascoignella* is endemic to the Indo-Malayan province (Jensen 1985; Swennen 2001), and the genus *Sohgenia* is endemic to the Central Pacific islands (Hamatani 1991). However, with one exception, these species have been described within the last 20 years, so they may have wider distributions.

Briggs (1995) considered the Hawaiian islands a separate region. The Hawaiian islands have a high endemicity (Ostergaard 1955; Kay 1967; present study), but the present study has shown that they also have a rather high similarity to the other islands of the Central and South Pacific (Table 7).

The islands of the South Pacific have been rather sporadically studied (Pease 1861, 1866, 1868, 1871; Eliot 1899; Risbec 1928, 1953; Burn 1966a; Miller 1969; Brodie & Brodie 1990; Gosliner 1995). Hence the total number of species as well as the number of endemics may be considerably higher. Gosliner & Draheim (1996) estimated that more than 40% of the opisthobranch species from Papua New Guinea are undescribed. For the Fiji Islands 30% of the species have not been identified to species level (Brodie & Brodie 1990). For the sacoglossans most of the old species are poorly described and need re-examination.

4. DISCUSSION

Sacoglossans are small, often cryptically colored species and they are therefore difficult to collect. This means that only a few biogeographic provinces have been thoroughly studied. In recent years international workshops and biodiversity programs have greatly increased the number of sacoglossans known from more remote localities, especially in tropical waters (JENSEN 1985, 1990, 1993b, 1997b,c, 1999, 2003; JENSEN & WELLS 1990; ICHIKAWA 1993; GOSLINER 1995; SWENNEN 1997, 2001; ORTEA & TEMPLADO 1988; ORTEA & ESPINOSA 1996, 2000, 2001, 2002; CABALLER et al. 2006; MUNIAN & ORTEA 1997). The present study has reviewed the existing information about sacoglossan distributions and analyzed the data for endemicity and similarity among provinces. Although the data are biased with regards to collecting efforts of a few highly active scientists, several patterns have emerged from these analyses. The collection bias is most obvious in the areas where few other observations have been made, e.g. the Brazilian region where basically all collections have been made by the Marcuses. However, the species richness and endemicity does not differ from that of other tropical regions with no collection bias. The same seems to be true for the Japanese fauna, where Baba has described most of the species. The sacoglossan fauna of the Indian sub-province has been studied by several taxonomists, but in this case endemicity seems remarkably high. One reason for this is that descriptions have been published in local journals and therefore overlooked by other taxonomists.

Overall the distributions of sacoglossans correspond to the biogeographic regions and provinces identified by BRIGGS (1995). The exceptions have been pointed out above. Some of the provinces identified contain less than 10 species, which means that just one endemic species will yield more than 10% endemicity. Obviously this cannot be used to make conclusions about their distinctiveness.

Table 8. Number of species and endemicity of the tropical provinces and sub-provinces of the Indo-West Pacific region.

Province/ subprovince	# species	# endemics (%)
Western Indian Ocean	27	5 (19)
Red Sea	10	2 (20)
India *s.l.*	20	10 (50)
Indo-Malayan	48	9 (19)
Central Pacific	51	4 (8)
Ryukyu	33	10 (30)
Hawaii	25	6 (24)
S Pacific	33	6 (18)
Northeast Australia + Great Barrier Reef	28	2 (7)
North and Northwestern Australia	23	4 (17)

The records listed in existing literature do not usually have longitude and latitude, and many locality names are ambiguous or oblivious. Consequently it has not been possible to construct a “degree-by-degree” plot of species distributions for analysis. Nevertheless, the latitudinal decrease in species diversity from warm to cold temperate provinces is spectacular. Sacoglossans are dietary specialists and the majority of species feed on siphonaceous green algae, which are much more abundant and diverse in tropical and warm temperate waters. The cold temperate sacoglossan faunas of the North Atlantic as well as the Northeast Pacific Ocean are mostly eurythermic species with wide latitudinal distributions, extending well into neighboring warm water regions; indices of inclusion are over 60% (Tables 3b, 4b). This is also seen in Japan (Table 5b) and southern Africa between the tropical western Indian Ocean and the warm temperate southwestern Africa (Table 7b), but not nearly as pronounced in Australia (Table 6b). This apparently supports Rapoport’s rule that species ranges in high latitudes are larger than in low latitudes. However, there are great differences between the provinces. The Northeast Pacific coldwater fauna is 43% of the tropical fauna, the Northeast Atlantic boreal fauna is 21% of the combined Lusitanian and Mediterranean fauna, and the Northwest Atlantic boreal fauna is only 12% of the Caribbean fauna.

The number of amphi-Atlantic species is relatively high, especially for the warm-water/tropical faunas (ORTEA et al. 1997; present study); 16 species (about 30%) occur in the Caribbean and the Lusitanian and/or Mediterranean provinces. However, amphi-Atlantic distributions for most of these species have only been recognized in recent years (TEMPLADO et al. 1990; ORTEA et al. 1988, 1998), and it cannot be excluded that human introductions are involved. Contrary to this, only one cold-temperate species, *Hermaea vancouverensis*, has an amphi-Pacific distribution. *Alderia modesta* has a circum-boreal/arctic distribution. *Elysiella pusilla* has recently been recorded from the Mexican-Panamanian province (BEHRENS & HERMOSILLO 2005). However, it cannot be excluded that this is a human introduction. The same is true for *Ercolania boodleae*, a Japanese species, which has been recorded from California (BEHRENS 1991); this may also be a misidentification (TROWBRIDGE 2002). The so-called circum-tropical species, *Elysia ornata* and *Ercolania coerulea*, are conspicuously absent from tropical eastern Pacific; they extend from the Caribbean to the South and/or Central Pacific islands. *Lobiger souverbii*, which has been synonymized with several Indo-West Pacific species (KAY 1964; BABA 1974; GOSLINER 1987a; GOSLINER et al. 1996), and which occurs in the Caribbean as well

Table 9. Distribution of species of the Oxynoacea, Plakobranchoidea and Limapontioidea in provinces supported by present study.

Region	Oxynoacea	Plakobranchoidea	Limapontioidea
NE Atlantic	0	1	10
Lusitanian	4	10	26
Mediterranean	3	11	24
NW Atlantic	0	2	4
Caribbean	6	25	23
NE Pacif. warm + cold	0	1	9
Mexican-Panamanian	5	6	12
SE Pacific	4	2	3
Hawaii	7	13	5
Japan cold temp.	3	11	12
Japan warm temp.	9	18	14
Ryukyu Islands	9	15	11
Australia, tropical	9	20	14
Australia, warm + cold	8	10	11
W Indian Ocean	9	18	8
India, Sri Lanka, Maldi.	8	8	4
Indo-Malaya	5	29	14
Central Pacific	10	25	16
SW Pacific	12	17	4

as Mexican-Panamanian province (Behrens 1991; Trowbridge 2002), may be the only truly circum-tropical species. Very few species are shared between the Caribbean and Mexican-Panamanian provinces, but there is probably a sister-taxon relationship between the East Pacific *Elysia diomedea* (formerly *Tridachiella diomedea*) and the Caribbean *E. crispata* (formerly *Tridachia crispata*) and *E. clarki*. Thus the Central American land bridge is as effective a geographical separation as the natural land barrier between the Red Sea and the Mediterranean. Also the few species occurring on both sides of the Isthmus of Panama may have arrived on the Pacific side as hitch-hikers on ships travelling through the Panama Canal.

The subdivision of the Indo-Polynesian province used in the present study may seem rather arbitrary. In many studies Papua New Guinea is considered a part of the Indo-Malayan sub-province, whereas it has been included in the South Pacific sub-province here. Only 14 species have been identified from Papua New Guinea, which is obviously an underrepresentation; Gosliner (1992) gives 61 species for this area, but most are undescribed or have not been identified to species. Only sacoglossans that have been identified to species level can be used for calculating similarities between different sub-provinces. The 14 species are almost all widespread species found in the Indo-Malayan as well as the Central Pacific sub-provinces. The one species that does not occur in these sub-provinces, *Elysia expansa*, has its main distribution in tropical Australia. Geologically Papua New Guinea has been associated with the Australian continent (Briggs 1995).

The number of species decreases with longitude to the west of the Central Pacific islands, from 51 through 48 in the Indo-Malayan sub-province to 20 in the Indian sub-province and 27 in the Western Indian Ocean province. The majority of species in the latter province have wide-spread distributions, whereas less than half the species in the Indian sub-province belong in this category. A less pronounced longitudinal decrease is seen from 33 species in the South Pacific islands through 28 in northeastern Australia to 23 in northwestern Australia.

The number of species of the Central and South Pacific islands, including Ryukyu, is at least 50% higher than the number of species in tropical East Pacific. This is in spite of the fact that the combined area of these islands is relatively small. On the other hand the endemicity of these islands is relatively low except in the Ryukyu Islands (Table 8). This means that insular isolation has not resulted in extensive speciation (or that subsequent dispersal has obscured such speciation). The high endemicity of Ryukyu is almost entirely attributable to one fairly recent publication: Ichikawa (1993).

Looking at distribution within subordinal taxa of the Sacoglossa, it is obvious that the shelled suborder Oxynoacea, which all feed exclusively on algae of the genus *Caulerpa*, is restricted by the distribution of this alga. In the North Atlantic shelled sacoglossans occur in Bermuda, but there is a questionable record of *Ascobulla fragilis* from the northern part of Spain (see above). In the East Pacific shelled species are found in the Panamanian region, but also in the southernmost part of the Gulf of California. In the West Pacific shelled species occur in the warm temperate region. The only places where shelled species occur in cold temperate waters are Victoria, southeastern Australia and the west coast of central Japan. These places also have species diversity of *Caulerpa* rivaling many tropical and warm temperate provinces (DOUMENGE 1995; PRUD'HOMME VAN REINE et al. 1996). The two nonshelled superfamilies, Plakobranchoidea and Limapontioidea, occur in all provinces where sacoglossans are found.

At the family level, the bivalved Juliidae are absent from the eastern Atlantic. Since they are common as fossils from this region, this must be due to extinction. Juliidae and Volvatellidae are rare in the Atlantic and eastern Pacific. On the other hand, Limapontioidea are highly diverse in the northeastern Atlantic and Mediterranean (Table 9). The least studied areas have the fewest Limapontioidae. This is probably due to the very small size (<10 mm) of most of these species. In tropical regions the number of Plakobranchioidea is always higher than the number of species in the other superfamilies. Plakobranchoidea are most diverse in the Caribbean region and in the Indo-Malayan and Central Pacific islands sub-provinces; tropical Australia also has a high proportion of this superfamily (Table 9).

Only rarely are more than two or three species of one genus found in one area. However, for the genera *Elysia* and *Thuridilla* many places have more than 5 species, and in a few cases more than 10 species may co-occur, though on different food algae. Whether this is due to sym- or parapatric speciation or dispersal following allopatric speciation, as suggested by GOSLINER (1995), cannot be deducted from existing information. Phylogenetic analysis, preferably including molecular data should be applied to these genera[1].

Some genera are restricted to one or a few neighboring biogeographic provinces. *Limapontia* only occurs in the Northeast Atlantic and Mediterranean region. This may also be the case for the genus *Calliopaea*, though the Japanese *Stiliger pusillus* has been tentatively assigned to this genus (BABA & HAMATANI 1970). The monotypic *Platyhedyle* only occurs in the Mediterranean (WAWRA 1979), whereas the genus *Gascoignella*, which has been assigned to the same family, Platyhedylidae (JENSEN 1996a), seems restricted to the South China Sea (JENSEN 1985; SWENNEN 2001). The monotypic genus *Olea* is restricted to the Northeast Pacific (TROWBRIDGE 2002). The genus *Bosellia* may have its natural distribution restricted to tropical and warm temperate Atlantic and Mediterranean (MARCUS 1973; FERNANDEZ-OVIES & ORTEA 1986), and the monotypic genus *Sohgenia* has only been found in the Central Pacific islands (HAMATANI 1991). Common to all of the above genera is that they have morphological characters that appear to be reduced compared to other genera in the same superfamilies; they either lack or have very reduced rhinophores, cerata or parapodia (or a combination of these). The genera *Roburnella, Plakobranchus* and *Pattyclaya* are Indo-west Pacific endemics, the former furthermore restricted to southern Australia, and *Julia* and *Elysiella* also occur in the eastern Pacific. Within the more speciose genera, many have few (1-3) representatives in the Atlantic Ocean, zero in the East Pacific, and the remaining species are Indo-West Pacific. This is seen in *Volvatella, Thuridilla* and *Costasiella*, indicating that the Atlantic fauna is a Tethyan relict fauna with little subsequent speciation, except in the genus *Elysia* in the Caribbean. However, the high number of limapontioid species seems to contradict this. It is possible that the lack of plakobranchoids first spurred a burst of speciation of limapontioids in the East Atlantic/Mediterranean, whereas the speciation in Caribbean *Elysia* may be a more recent phenomenon.

The present study is a preliminary analysis of biogeographic affinities of sacoglossan opisthobranchs. Nevertheless several patterns have been identified, which should be further investigated using phylogenetic analyses. Also, some obvious gaps in the existing knowledge as well as conflicting and/or questionable records have been identified. There is an urgent need to describe the undescribed species known from the Indo-West Pacific region and to collect sacoglossans from poorly studied regions. Finally, several new hypotheses emerge from the present analyses, which should be tested in the future: the genus *Elysia* has speciated within the Caribbean; warm temperate Australia and Japan are centers of speciation; the appearance of several Caribbean species in the Canary Islands is due to human activities.

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APPENDIX

List of nominal species of recent Sacoglossa, authorship and type localities. Species are arranged alphabetically within families and superfamilies. Valid species (and species for which synonymy has been contested) are listed with their current generic name. Species considered invalid in the present study are marked with an *.

Species	Author	Type locality
Oxynoacea		
Volvatellidae		
Ascobulla californica	(Hamatani, 1971)	Gulf of California
Ascobulla fischeri	(Adams & Angas, 1864)	"South Australia"
Ascobulla fragilis	(Jeffreys, 1856)	Mediterranean
Ascobulla japonica	(Hamatani, 1969)	Kii, Middle Japan
Ascobulla? pusilla	(Nevill & Nevill, 1869)	Sri Lanka
Ascobulla souverbiei	(Montrouzier in Souverbie & Montrouzier, 1874)	New Caledonia
*Ascobulla? systremma**	(Melvill, 1918)	Gulf of Oman
Ascobulla ulla	(Marcus & Marcus, 1970)	E of Santos, Brazil
*Ascobulla? turtoni**	(Bartsch, 1915)	South Africa
Volvatella angeliniana	Ichikawa, 1993	Sesoko Isl., Ryukyu
Volvatella australis	Jensen, 1997	Darwin Harbour, N Australia
Volvatella ayakii	Hamatani, 1972	Kii, Middle Japan
Volvatella bermudae	Clark, 1982	Bermuda
Volvatella candida	Pease, 1868	French Polynesia
Volvatella cincta	Nevill & Nevill, 1869	Sri Lanka
Volvatella elioti	(Evans, 1950)	Zanzibar
Volvatella evansi	(Kay, 1961)	Oahu, Hawaii
Volvatella ficula	Burn, 1966	Fiji
Volvatella fragilis	Pease, 1860	Sandwich Islands
*Volvatella kawamurai**	Habe, 1946	Japan
Volvatella laguncula	Sowerby, 1894	Port Elizabeth, S Africa
Volvatella omega	(Melvill, 1918)	Gulf of Oman
Volvatella pyriformis	Pease, 1868	Huaheine, French Polynesia
Volvatella ventricosa	Jensen & Wells, 1990	Albany, SW Australia
Volvatella vigourouxi	(Montrouzier, 1861)	New Caledonia
Volvatella viridis	Hamatani, 1976	Amami Islands, Japan
Juliidae		
Berthelinia (Midorigai) australis	(Burn, 1960)	Torquay, Victoria, Australia
Berthelinia (Tamanovalva) babai	(Burn, 1965)	Torquay, Victoria, Australia
Berthelinia caribbea	Edmunds, 1963	Port Royal, Jamaica
Berthelinia chloris	(Dall, 1918)	Baja California, W Mexico
*Berthelinia corallensis**	Hedley, 1920	Queensland, Australia
Berthelinia darwini	Jensen, 1997	Darwin Harbour, N Australia
Berthelinia (Tamanovalva) fijiensis	(Burn, 1966)	Fiji
Berthelinia ganapati	Sarma, 1975	SE India
Berthelinia (Tamanovalva) limax	(Kawaguti & Baba, 1959)	Seto, Japan
Berthelinia pseudochloris	Kay, 1964	Kauai, Hawaii
Berthelinia rottnesti	Jensen, 1993	Rottnest Island, SW Australia
Berthelinia schlumbergeri	Dautzenberg, 1895	Madagascar
Berthelinia (Edenttellina) typica	(Gatliff & Gabriel, 1911)	Port Phillip, Victoria, Australia
Berthelinia waltairensis	Sarma, 1975	SE India
*Julia borbonica**	(Deshayes, 1863)	Reunion
Julia burni	Sarma, 1975	Andaman Islands, India
*Julia cornuta**	(De Folin, 1867)	Mauritius
*Julia equatorialis**	Pilsbry & Olsson, 1944	N of Mancara, Peru
Julia exquisita	Gould, 1862	Hawaiian Islands
Julia japonica	Kuroda & Habe, 1951	Wakayama, Honshu, Japan
Julia mishimaensis	Kawaguti & Yamasu, 1982	Yamaguchi Pref. Japan
Julia thecaphora	(Carpenter, 1857)	Mazatlán, Mexico(?)
Julia zebra	Kawaguti 1981	Yamaguchi Pref. Japan
Oxynoidae		
*Icarus gravesii**	Forbes, 1844	Aegean Sea
*Lobiger corneus**	Mörch, 1863	? (Cuming collection)

_Lobiger cumingi_*	(A. Adams, 1850)	Puerto St. Elena, W Colombia
Lobiger nevilli	Pilsbry, 1896	n.n. for L. viridis G. &. H. Nevill, 1869
_Lobiger pellucidus_*	A. Adams, 1854	unknown (Cuming collection)
_Lobiger philippi_*	Krohn, 1847	Sicily, Italy
_Lobiger pilsbryi_*	Schwengel, 1941	Sanibel Isl., Florida
_Lobiger picta_*	Pease, 1868	Huaheine, French Polynesia
Lobiger sagamiensis	Baba, 1952	Sagami Bay, Japan
Lobiger serradifalci	(Calcara, 1840)	Sicily, Italy
Lobiger souverbii	Fischer, 1856	Guadeloupe
Lobiger viridis	Pease, 1863	Huahine
_Lobiger viridis_*	Nevill & Nevill, 1869	Sri Lanka
_Lophocercus krohnii_*	A. Adams, 1854	Hawaiian Islands (Sandwich Islands)
_Lophocercus sieboldii_*	Krohn, 1847	Messina, Italy
Lophopleurella capensis	(Thiele, 1912)	S Africa
_Oxynoe aguayoi_*	Jaume, 1945	Cuba
Oxynoe antillarum	Mörch, 1863	St. Thomas, USVI
Oxynoe azuropunctata	Jensen, 1980	Florida
Oxynoe benchijigua	Ortea, Moro & Espinosa, 1999	Canary Islands
_Oxynoe brachycephalus_*	Mörch, 1863	Based on figure
Oxynoe delicatula	Nevill & Nevill, 1869	Sri Lanka
_Oxynoe hargravesi_*	Adams, 1872	New Hebrides
Oxynoe kabirensis	Hamatani, 1980	Ishigaki Isl., Ryukyu Islands
_Oxynoe natalensis_*	Smith, 1903	Port Elizabeth, S Africa
Oxynoe olivacea	Rafinesque, 1814	Sicily, Italy
Oxynoe panamensis	Pilsbry & Olsson, 1943	Bocas Isl., Panama
Oxynoe viridis	(Pease, 1861)	Sandwich Islands
Roburnella wilsoni	(Tate, 1889)	Port Phillip Bay, Victoria, Australia

Plakobranchacea

Plakobranchidae

_Actaeon elegans_*	de Quatrefages, 1844	St. Vaast, France
_Aplysiopterus neapolitanus_*	delle Chiaje, 1830	Napoli, Italy
_Elisia marmorata_*	Cantraine, 1835	Livorno, italy
Elysia abei	Baba, 1955	Sagami Bay, Japan
_Elysia albomarginata_*	Trinchese, 1869	Italy
Elysia amakusana	Baba, 1955	Sagami Bay, Japan
Elysia atroviridis	Baba, 1955	Sagami Bay, Japan
Elysia australis	(Quoy & Gaimard, 1832)	Port Jackson, Sydney, NSW
Elysia babai	Pruvot-Fol, 1946	Ryukyu Islands
Elysia bangtawaensis	Swennen, 1997	Pattani, Gulf of Thailand
_Elysia bedeckta_*	MacFarland, 1966	Monterey Bay, California
Elysia bella[3]	(Pease, 1860)	Hawaii
Elysia bennettae	Thompson, 1973	Heron Island, GBR
Elysia canguzua	Marcus, 1955	NE of Santos, Brazil
Elysia catulus	(Gould, 1870)	Massachusetts, USA
_Elysia cauze_*	Marcus, 1957	NE of Santos, Brazil
Elysia chilkensis	Eliot, 1916	Chilka Lake, India
Elysia chitwa	Marcus, 1955	NE of Santos, Brazil
Elysia chlorotica	Gould, 1870	Massachusetts, USA
Elysia clarki	Pierce et al., 2006	Florida
_Elysia clena_*	Marcus & Marcus, 1970	?Curacao/?Barbados
Elysia coodgeensis	(Angas, 1864)	Port Jackson, Sydney, NSW
_Elysia cornigera_*	Nuttall, 1989	Spanish Harbor Key, FL
Elysia crispata	Mörch, 1863	St. Croix, USVI
_Elysia cyanea_*	Mamo in Caruana, 1867	Malta
Elysia degeneri	Ostergaard, 1955	Oahu, Hawaii
Elysia diomedea	(Bergh, 1894)	Lower California
_Elysia dubia_*	Eliot, 1904	Zanzibar
_Elysia duis_*	Marcus & Marcus, 1967	Biscayne Bay, Florida
_Elysia elsiae_*	Ostergaard, 1955	Waikiki, Hawaii
Elysia eugeniae	Ortea & Espinosa, 2002	Manzanillo, Costa Rica (Carib)
Elysia evelinae	Marcus, 1957	NE of Santos, Brazil
Elysia kushimotoensis	Baba, 1957	Kushimoto, Kii, Japan
Elysia expansa	(O'Donoghue, 1924)	Abrolhos Islands, NW Australia
_Elysia faustula_*	Bergh, 1872	Masoloc, Philippines

Elysia fezi	Vilella, 1968	Barcelona, Spain
Elysia filicauda	Jensen & Wells, 1990	Albany, SW Australia
Elysia flava	Verrill, 1901	Bermuda
Elysia flavipunctata	Ichikawa, 1993	Ishigaki Isl., Ryukyu
Elysia flavomacula	Jensen, 1990	Hong Kong
Elysia furvacauda	Burn, 1958	Torquay, Victoria, Australia
*Elysia fusca**	Philippi, 1844	Palermo, Italy
Elysia gordanae	Thompson & Jaklin, 1988	Rovinj, Yugoslavia
Elysia grandifolia	Kelaart, 1857	Sri Lanka
Elysia grandis[3]	Bergh, 1872	Palau? (Pelew)
Elysia haingsisiana[3]	Bergh, 1905	Haingsisi
*Elysia halimedae**	Macnae, 1954	Port Alfred, S Africa
Elysia hamatanii	Baba, 1957	Seto, Japan
Elysia hedgpethi	Marcus, 1961	Tomales Bay, California
Elysia hendersoni	Eliot, 1899	Samoa
Elysia hetta	Perrone, 1990	Gulf of Taranto, Italy
Elysia hirasei	Baba, 1955	Sagami Bay, Japan
Elysia japonica	Eliot, 1913	Japan
*Elysia latipes**	Marcus, Er. & Marcus, Ev. 1960	Maldives
Elysia leucolegnote	Jensen, 1990	Hong Kong
Elysia lobata	Gould, 1852	Hawaii
*Elysia macnaei**	Ev. Marcus, 1980	Japan?/Australia?
Elysia maoria	Powell, 1937	Auckland, NZ
Elysia margaritae	Fez, 1962	Valencia, Spain
*Elysia marginata**	(Pease, 1871)	Huaheine, French Polynesia
Elysia minima	Ichikawa, 1993	Kuro Isl., Ryukyu
*Elysia minuta**	(Sars, 1835)	Bergensund, Norway
Elysia nealae	Ostergaard, 1955	Waikiki, Hawaii
Elysia nigrocapitata	Baba, 1957	?Osaka/?Seto/?Tsurugu/?Toyama Bay Japan
Elysia nigropunctata	(Pease, 1871)	Tahiti
Elysia nisbeti	Thompson, 1977	Jamaica
Elysia obtusa	Baba, 1938	Seto, Japan
*Elysia ocellata**	Pease, 1860	Hawaii
Elysia oerstedii	Mørch, 1859	Puntarenas, Central America
Elysia ornata	(Swainson, 1840)	West Indies
*Elysia ornata**	(Pease, 1860)	Hawaii
*Elysia pagenstecheri**	Marcus, Ev., 1982	Sète, Mediterranean
Elysia papillosa	Verrill, 1901	Bermuda
Elysia patagonica	Munian & Ortea, 1997	San Jorge Gulf, Argentina (45d58'S; 67d34'W)
Elysia patina	Marcus, 1980	Florida Keys
Elysia pilosa	Risbec, 1928	New Caledonia
Elysia pratensis	Ortea & Espinosa, 1996	Eastern part of Yucatan, Mexico
*Elysia pruvotae**	Risbec, 1953	New Caledonia
Elysia punctata	Kelaart, 1857	Sri Lanka
Elysia purchoni	Thompson, 1977	Jamaica
Elysia rufescens	(Pease, 1871)	Tahiti
Elysia serca	Marcus, 1955	NE of Santos, Brazil
Elysia setoensis	Hamatani, 1968	Seto, Japan
Elysia siamensis	Swennen, 1997	Pattani, Gulf of Thailand
Elysia slimora	Marcus & Marcus, 1966	near Sao Tome, W Africa
*Elysia splendida**	Grube, 1861	Cherso, N Adriatic
Elysia subornata	Verrill, 1901	Bermuda
Elysia sugashimae	Baba, 1955	Sagami Bay, Japan
Elysia thompsoni	Jensen, 1993	Rottnest Island, SW Australia
Elysia timida	Risso, 1818	Nice, France Mediterr.
Elysia tokarensis	Baba, 1957	Tokara Islands, Kyushu, Japan
Elysia tomentosa	Jensen, 1997	Abrolhos Islands, NW Australia
Elysia translucens	Pruvot-Fol, 1957	Banyuls, France Mediterr.
Elysia trilobata	Heller & Thompson, 1983	Red Sea
Elysia trisinuata	Baba, 1949	Sagami Bay, Japan
Elysia tuca	Marcus & Marcus, 1967	Biscayne Bay, Florida
*Elysia (Elysiella) verrilli**	Thiele, 1931	n.n. for Elysia (Elysiella catula Verrill
Elysia verrucosa	Jensen, 1985	Hong Kong

Elysia viridis	(Montagu, 1804)	Devonshire, UK
*Elysia viridissima**	Trinchese, 1869	Italy
Elysia vreelandae	Marcus & Marcus, 1970	W Mexico
Elysia yaeyamana	Baba, 1936	Ishigakishima, Ryukyu
Elysia zuleicae	Ortea & Espinosa, 2002	Cuba
Elysiella pusilla	Bergh, 1872	Aibukit, ?Palau (Palaos)
Elysiella stylifera	Jensen, 1997	Darwin Harbour, N Australia
Elysiobranchus mercieri	Pruvot-Fol, 1930	New Caledonia
Elysiobranchus ryukyuensis	Ichikawa, 1993	Sesoko Isl., Ryukyu
Pattyclaya arena	Carlson & Hoff, 1978	Guam
Pattyclaya brycei	Jensen & Wells, 1990	Albany, SW Australia
*Placobranchus argus**	Bergh, 1872	Honolulu, Hawaii
*Placobranchus caminguinus**	Bergh, 1872	Luzon, Philippines
*Placobranchus chlorophagus**	Bergh, 1878	Huaheine
*Placobranchus gracilis**	Pease, 1871	Tahiti
*Placobranchus guttatus**	Stimpson, 1858	Ryukyu Islands
*Plakobranchus ianthobapsus**	Gould, 1852	Honolulu, Hawaii
*Placobranchus laetus**	Bergh, 1872	Masoloc, Philippines
Plakobranchus ocellatus	van Hasselt, 1824	Sunda Strait
*Placobranchus priapinus**	Bergh, 1872	Bohol, Philippines
*Placobranchus punctulatus**	Bergh, 1872	Masoloc, Philippines
*Placobranchus variegatus**	Pease, 1871	Huaheine, French Polynesia
Thuridilla albopustulosa	Gosliner, 1995	Madang, PNG
Thuridilla bayeri	(Marcus, 1965)	Marshall Islands
Thuridilla carlsoni	Gosliner, 1995	Madang, PNG
Thuridilla coerulea	(Kelaart, 1857)	Sri Lanka
Thuridilla decorata	(Heller & Thompson, 1983)	Red Sea
Thuridilla flavomaculata	Gosliner, 1995	Luzon, Philippines
Thuridilla gracilis	(Risbec, 1928)	New Caledonia
Thuridilla hoffae	Gosliner, 1995	Madang, PNG
Thuridilla hopei	(Verany, 1853)	Nice, France Mediterr.
Thuridilla indopacifica	Gosliner, 1995	Aldabra Atoll
Thuridilla kathae	Gosliner, 1995	Madagascar
Thuridilla lineolata	(Bergh, 1905)	Saleyer
Thuridilla livida	(Baba, 1955)	Sagami Bay, Japan
Thuridilla mazda	Ortea & Espinosa, 2000	Manzanillo, Costa Rica (Carib)
Thuridilla moebii	(Bergh, 1888)	Mauritius
Thuridilla multimarginata	Gosliner, 1995	Midway Atoll
Thuridilla neona	Gosliner, 1995	Lanai, Hawaii
Thuridilla picta	(Verrill, 1901)	Bermuda
Thuridilla ratna	(Marcus, 1965)	Palau
Thuridilla splendens	(Baba, 1949)	Sagami Bay, Japan
Thuridilla thysanopoda[3]	(Bergh, 1905)	Tual, Kei Islands, Indonesia
Thuridilla undula	Gosliner, 1995	Madang, PNG
Thuridilla vatae	(Risbec, 1928)	New Caledonia
Thuridilla virgata	(Bergh, 1888)	Mauritius
*Tridachia schrammi**	Mörch, 1863	Guadeloupe
Boselliidae		
Bosellia cohellia[2]	Marcus, 1978	?Red Sea/?Mediterranean
Bosellia corinneae	Marcus, 1973	Key Biscayne, Florida
Bosellia leve	Fernandez-Ovies & Ortea, 1986	Lanzarote, Canary Islands
Bosellia marcusi	Marcus, 1972	Grassy Key & Miami, FL
Bosellia mimetica	Trinchese, 1890	Capri, Italy
Platyhedylidae		
Gascoignella aprica	Jensen, 1985	Hong Kong
Gascoignella jabae	Swennen, 2001	Pattani, Gulf of Thailand
Gascoignella nukuli	Swennen, 2001	Pattani, Gulf of Thailand
Platyhedyle denudata	Salvini-Plawen, 1973	Livorno, italy
Limapontioidea		
Polybranchidae (=Caliphyllidae)		
Caliphylla mediterranea	(A. Costa, 1867)	Napoli, Italy
*Caliphylla tricolor**	Trinchese, 1879	Mediterranean
Cyerce antillensis	Engel, 1927	Tobago(?), Westindien

Cyerce cristallina	(Trinchese, 1881)	Napoli, Italy
Cyerce? edmundsi	Thompson, 1977	Jamaica
Cyerce elegans	Bergh, 1871	Palau? (Palaos)
Cyerce graeca	Thompson, 1988	Greek Ionian Sea
Cyerce habanensis	Ortea & Templado, 1988	Cuba
*Cyerce jheringi**	Pelseneer, 1892	Napoli, Italy
Cyerce kikutarobabai	Hamatani, 1976	Amami Islands, Japan
Cyerce nigra	Bergh, 1871	Palau? (Palaos)
Cyerce nigricans	(Pease, 1866)	Pacific Islands
Cyerce orteai	Valdès & Camacho, 2000)	Puntarenas, Costa Rica
Cyerce pavonina	Bergh, 1888	Mauritius
Cyerce verdensis	Ortea & Templado 1990	Cape Verde
Mourgona germaineae	Marcus & Marcus, 1970	Puerto Rico (aquarium)
Mourgona murca	Marcus & Marcus, 1970	Curacao
Mourgona osumi	Hamatani, 1994	Amami-Oshima Island, SW Japan
Polybranchia borgnini	(Trinchese, 1895)	Mediterranean
Polybranchia orientalis	(Kelaart, 1858)	Sri Lanka
Polybranchia pallens	(Burn, 1957)	Queenscliff, Victoria, Australia
Polybranchia papillosa	(Pease, 1866)	Pacific Islands
Polybranchia pellucida	Pease, 1860	Hawaii
Polybranchia prasinus	(Bergh, 1871)	Luzon, Philippines
*Polybranchia rubicundus**	(Bergh, 1871)	Tor, Red Sea
Polybranchia viridis	(Deshayes, 1857)	Guadeloupe
Polybranchia westralis	Jensen, 1993	Rottnest Island, SW Australia
Sohgenia palauensis	Hamatani, 1991	Palau

Hermaeidae

Aplysiopsis brattstroemi	(Marcus, 1959)	Chile (23d39'S; 70d25'W)
Aplysiopsis elegans	(Deshayes, 1835)	Banyuls, France Mediterr.
Aplysiopsis enteromorphae	(Cockerell & Eliot, 1905)	San Pedro, California(?)
Aplysiopsis formosa	Pruvot-Fol, 1953	Temara, Marocco
*Aplysiopsis maculosa**	(Trinchese, 1874)	Genova, Italy
Aplysiopsis minor	(Baba, 1959)	Toyama Bay, Japan
Aplysiopsis nigra	(Baba, 1949)	Sagami Bay, Japan
Aplysiopsis orientalis	(Baba, 1949)	Sagami Bay, Japan
Aplysiopsis sinusmensalis	(Macnae, 1954)	Table Bay, S Africa
*Aplysiopsis smithi**	(Marcus, 1961)	Tomales Bay, California
Aplysiopsis toyamana	(Baba, 1959)	Toyama Bay, Japan
*Aplysiopsis zebra**	Clark, 1982	Florida
Hermaea bifida	(Montagu, 1816)	Devonshire, UK
Hermaea boucheti	Cervera, Garcia-Gomez & Ortea, 1991	Pontevedra, SW Spain
*Hermaea carminis**	Fez, 1962	Valencia, Spain
Hermaea coirala	Marcus, 1955	NE of Santos, Brazil
Hermaea cruciata	Gould, 1870	Massachusetts, USA
Hermaea evelinemarcusae	Jensen, 1993	Rottnest Island, SW Australia
Hermaea hillae	Marcus & Marcus, 1967	Sonora, W Mexico
*Hermaea lutescens**	A. Costa, 1866	Napoli, Italy
*Hermaea minor**	Bergh, 1888	Mauritius
Hermaea noto	(Baba, 1959)	?Noto Peninsula/?Toyama Bay Japan
Hermaea oliviae	(MacFarland, 1966)	Monterey Bay, California
Hermaea paucicirra	Pruvot-Fol, 1953	Marocco
*Hermaea polychroma**	(Hesse, 1873)	Brest
Hermaea vancouverensis	O'Donoghue, 1924	Vancouver Isl., Canada
Hermaea variopicta	(A. Costa, 1869)	Napoli, Italy
*Hermaea venosa**	Lovén, 1845	Bohuslän, Sweden
Hermaea wrangeliae	(Ichikawa, 1993)	Kuro Isl., Ryukyu
Hermaea zosterae	(Baba, 1959)	Amakusa, Japan
*Physopneumon carneum**	A. Costa, 1862	Mediterranean

Limapontiidae

Alderella comosa	(Costa, 1867)	Napoli, Italy
*Alderia harvardiensis**	Gould, 1870	Massachusetts, USA
Alderia modesta	(Lovén, 1844)	Bohuslän, Sweden
*Alderia scaldiana**	Nyst, 1855	Scheldt estuary, Netherlands
Alderia uda	Marcus, Ev. & Marcus, Er., 1956)	SW of Santos, Brazil
Alderia willowi	Krug, Ellingson, Burton & Valdés, 2007	San Pedro, California

Alderiopsis garfio	Caballer, Ortea & Espinosa, 2006	Cuba
Alderiopsis nigra	(Baba, 1937)	Amakusa, Japan
Calliopaea bellula	d'Orbigny, 1837	France
Calliopaea oophaga	Lemche, 1974	Samsø, Kattegat, DK
*Calliopaea souleyeti**	Verany, 1853	Nice, France Mediterr.
*Cenia cocksii**	Alder & Hancock, 1848	Falmouth, UK
*Cenia corrugata**	Alder & Hancock, 1848	Falmouth, UK
*Chalidis coeruleus**	de Quatrefages, 1844	Ile de Bréhat, France
*Chalidis nigricans**	Alder & Hancock, 1847	Falmouth, UK
Costasiella formicaria	(Baba, 1959)	Amakusa, Japan
Costasiella illa	(Marcus, 1965)	Caroline Islands, Micronesica
Costasiella iridophora	Ichikawa, 1993	Kuro Isl., Ryukyu
Costasiella kuroshimae	Ichikawa, 1993	Kuro Isl., Ryukyu
*Costasiella lilianae**	(Marcus, Ev. & Marcus, Er., 1969	NE of Santos, Brazil
Costasiella mandurahae	Jensen, 1997	Darwin Harbour, N Australia
Costasiella nonatoi	Marcus & Marcus, 1960	NE of Santos, Brazil
Costasiella ocellifera	(Simroth, 1895)	Bermuda
Costasiella pallida	Jensen, 1985	Hong Kong
Costasiella paweli	Ichikawa, 1993	Miyako Isl., Ryukyu
Costasiella rubrolineata	Ichikawa, 1993	Ishigaki Isl., Ryukyu
Costasiella usagi	Ichikawa, 1993	Ishigaki Isl., Ryukyu
Costasiella vegae	Ichikawa, 1993	Ishigaki Isl., Ryukyu
Costasiella virescens	Pruvot-Fol, 1951	Banyuls, France Mediterr.
*Custiphorus vesiculosus**	Deshayes, 1853	?
*Embletonia mariae**	Meyer & Möbius, 1865	Kieler Bucht
Ercolania boodleae	(Baba, 1938)	Seto, Japan
Ercolania coerulea	Trinchese, 1892	Napoli, Italy
*Ercolania costai**	Pruvot-Fol, 1951	?Banyuls/?Monaco, Mediterranean
*Ercolania cricetae**	(Marcus & Marcus, 1970)	Curacao
Ercolania evelinae	(Marcus, 1959)	Chile (53d22'S; 70d57'W)
*Ercolania emarginata**	Jensen, 1985	Hong Kong
Ercolania endophytophaga	Jensen, 1999	Rottnest Island, SW Australia
Ercolania erbsus	(Marcus & Marcus, 1970)	Madagascar
Ercolania felina	(Hutton, 1882)	New Zealand
*Ercolania funerea**	(Costa, 1867)	Napoli, Italy
Ercolania fuscata	(Gould, 1870)	Massachusetts, USA
Ercolania gopalai	(Rao, 1937)	Madras, E India
Ercolania irregularis	(Eliot, 1904)	Zanzibar
Ercolania lozanoi	Ortea, 1981	Tenerife, Canary Islands
Ercolania margaritae	Burn, 1974	Point Lonsdale, Victoria, Australia
Ercolania nigra	(Lemche, 1936)	Nyborg Fjord, DK
*Ercolania nigrovittata**	(A. Costa, 1866)	Napoli, Italy
*Ercolania nigrovittata**	(Rao & Rao, 1963)	Gulf of Mannar, SE India
*Ercolania pancerii**	Trinchese, 1872	Genova, Italy
Ercolania pica	(Annandale & Prashad, 1922)	Chilka Lake, India
Ercolania raorum	(Marcus & Marcus, 1970)	Gulf of Mannar, SE India
Ercolania selva	Ortea & Espinosa, 2001	Manzanillo, Costa Rica (Carib)
Ercolania siottii	Trinchese, 1872	Genova, Italy
Ercolania subviridis	(Baba, 1959)	Toyama Bay, Japan
*Ercolania talis**	(Marcus & Marcus, 1956)	SW of Santos, Brazil
Ercolania tentaculata	(Eliot, 1917)	Singgora, SE Thailand
Ercolania translucens	Jensen, 1993	Rottnest Island, SW Australia
*Ercolania trinchesii**	Pruvot-Fol, 1951	?Banyuls/?Monaco, Mediterranean
*Ercolania uziellii**	Trinchese, 1872	Genova, Italy
*Ercolania vanellus**	Marcus, 1957	E of Santos, Brazil
Ercolania varians	(Eliot, 1904)	Zanzibar
Ercolania viridis	(A. Costa, 1866)	Napoli, Italy
Ercolania zanzibarica	Eliot, 1903	E Zanzibar
Limapontia capitata	(Müller, 1773)	Baltic Sea
*Limapontia cornuta**	Giard, 1873	?
Limapontia depressa	Alder & Hancock, 1862	Sunderland, UK
*Limapontia nigra**	Johnston, 1836	Berwick Bay, UK
Limapontia senestra	(de Quatrefages, 1844)	Ile de Bréhat, France
Limapontia zonata[1]	(Girard, 1852)	Massachusetts, USA
Olea hansineensis	Agersborg, 1923	Friday Harbor, Washington

*Placida aoteana**	(Powell, 1937)	Auckland, NZ
*Placida babai**	Marcus, Ev., 1982	Seto, Japan
Placida brevicornis	(A. Costa, 1867)	Napoli, Italy
*Placida capensis**	Macnae, 1954	Cape Province, S Africa
Placida cremoniana	(Trinchese, 1892)	Napoli, Italy
Placida daguilarensis	Jensen, 1990	Hong Kong
Placida dakariensis	(Pruvot-Fol, 1953)	Dakar, Senegal
Placida dendritica	(Alder & Hancock, 1843)	Torbay, UK
Placida fralila	Burn, 1966	Queensland, Australia
Placida kingstoni	Thompson, 1977	Jamaica
*Placida ornata**	(MacFarland, 1966)	Monterey Bay, California
Placida saronica	(Thompson, 1988)	Greek Aegean Sea
Placida tardyi	(Trinchese, 1873)	Genova, Italy
Placida verticillata	Ortea, 1981	Tenerife, Canary Islands
Placida viridis	(Trinchese, 1873)	Genova, Italy
Stiliger akkeshiensis	Baba, 1935	Akkeshi Bay, Hokkaido, Japan
Stiliger aureomarginatus	Jensen, 1993	Rottnest Island, SW Australia
Stiliger berghi	Baba, 1937	Tomioka, Amakusa, Japan
Stiliger fuscovittatus	Lance, 1962	San Diego, California
Stiliger llerai	Ortea, 1981	Tenerife, Canary Islands
Stiliger pusillus	Baba, 1959	Osaka Bay, Japan
Stiliger smaragdinus	Baba, 1949	Sagami Bay, Japan
Stiliger ornatus	Ehrenberg, 1828	Red Sea
Stiliger vossi	Marcus & Marcus, 1960	Upper Florida Keys
Stiliger? viridis[2]	(Kelaart, 1858)	Sri Lanka

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[1] This species is probably a flatworm rather than a sacoglossan.

[2] The taxonomic status of this species is so uncertain that it has been omitted from the analyses.

[3] This species has been omitted from the analyses due to lack of information.

[4] Since the type locality is uncertain, this species has been omitted from the analyses.

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Re-description of a female *Pontohedyle brasilensis* (Rankin, 1979), a junior synonym of the Mediterranean *P. milaschewitchii* (Kowalevsky, 1901) (Acochlidia, Gastropoda)*

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Abstract. Currently 27 species are considered to be valid in the still enigmatic opisthobranch group of the Acochlidia. The taxonomic status of the acochlidian species, *Pontohedyle brasilensis* (Rankin, 1979), remained unclear due to a lack of primary data. The present study provides the first structural and some histological data on a female *P. brasilensis* from northern Brazil. The female genital system is reconstructed 3-dimensionally from serial semithin sections using AMIRA software. Our new results are compared with published data on a male *P. brasilensis* from southern Brazil and on *P. milaschewitchii* (Kowalevsky, 1901) from the Mediterranean and Black Sea; in absence of morphological differences we consider *P. brasilensis* as a junior synonym. The genus *Pontohedyle* thus comprises two valid species, the Atlantic/Mediterranean *P. milaschewitchii* and the tropical Indopacific *P. verrucosa* (Challis, 1970). Both possess unique bow-shaped, flattened oral tentacles, which are diagnostic for the genus and, thus, a probable autapomorphy.

Keywords. Mollusca, Opisthobranchia, taxonomy, morphology, anatomy, 3D reconstruction.

1. INTRODUCTION

Currently, 27 nominal acochlidian species are considered to be valid (SOMMERFELDT & SCHRÖDL 2005) which were conventionally classified into 12 different genera in 6 families (WAWRA 1987). All acochlidians have a characteristic shell-less body with a head-foot complex that can be at least partly retracted into a more or less elongate visceral hump. Most species belong to tiny members of worldwide coastal mesopsammic communities, while others are inhabitants of brackish waters or even limnic (see NEUSSER & SCHRÖDL 2007). Uniquely within the usually hermaphroditic opisthobranchs, microhedylid acochlidian species have separate sexes. While most acochlidians have two pairs of cephalic tentacles, a few gonochoristic species lack any rhinophores, i.e. of the genera *Ganitus* Marcus, 1953 and *Pontohedyle* Golikov & Starobogatov, 1972. There are three nominal *Pontohedyle* species: the tropical Indopacific *P. verrucosa* (Challis, 1970), the Atlantic/ Mediterranean species *P. milaschewitchii* (Kowalevsky, 1901), and the Atlantic *P. brasilensis* (Rankin, 1979) with uncertain taxonomic status.

Pontohedyle milaschewitchii was originally described from the Black Sea (KOWALEVSKY 1901) and later found throughout the Mediterranean (see HADL et al. 1969; JÖRGER et al. in press; POIZAT 1984; WAWRA 1986). Additionally, MARCUS & MARCUS (1954) described one single male specimen of *P. milaschewitchii* from Ilhabela (São Paulo State), the coast of southern Brazil. Solely based on that literature information, RANKIN (1979) established the new genus and species *Gastrohedyle brasilensis* and separated it from the Mediterranean *P. milaschewitchii* (as *Mancohedyle*); her diagnosis of *P. milaschewitchii* then was limited to the original description by KOWALEVSKY (1901). ARNAUD et al. (1986) listed *Gastrohedyle brasilensis* as *Pontohedyle brasilensis* with a question mark, and WAWRA (1987) regarded it as a probable synonym of *P. milaschewitchii*, however without giving any discussion on an entire set of putative external and internal morphological differences that were raised by RANKIN (1979).

Unfortunately, anatomical information of *P. brasilensis* is restricted to a single male specimen. This type specimen of *P. brasilensis* has not been discovered in the Marcus' collection of the Museu de Zoologia da Universidade de São Paulo (C. Magenta, São Paulo, pers. comm. 2006), and thus appears to be lost. Specimens of *Pontohedyle* from Brazil remain very rare. Even after exhaustive search at the original location, MARCUS & MARCUS (1954) were not able to rediscover further specimens. We conducted collections at Ilhabela, the type locality of *P. brasilensis*, along the coast of Santa Catarina, Paraná and São Paulo State, southern Brasil, and at many sites in Pernambuco and Paraíba, northern Brazil. This search only resulted in two specimens, one of them usable for histological analysis.

The present study provides the first structural and histological data on a female *Pontohedyle* from northern Brazil. The taxonomy of *P. brasilensis* is revised by critically comparing our results with the published data on *P. brasilensis* from Brazil and *P. milaschewitchii* from the Mediterranean.

2. MATERIAL AND METHODS

Two *Pontohedyle* specimens were extracted from sand samples (see SCHRÖDL 2006 for method of extraction), collected by scuba diving on the northern coast of Brazil (approx. 5 km off Porto de Galinhas, at 20 m depth) in January 2004. One retracted and damaged specimen was used for molecular analysis. The posterior part of the visceral hump of the second specimen was also damaged. The specimens were slowly anaesthetised using 7 % isotonic $MgCl_2$ solution and fixed in 75 % ethanol. The preserved specimen used for histological analysis in the present study was transferred into Bouin solution for decalcification and afterwards stained with 0.5 % safranin. Then it was dehydrated by a graded acetone series and embedded in Spurr´s low viscosity epoxy resin (SPURR 1969) for sectioning. The epoxy resin block was cut at 1.5 µm with a rotation-microtome (Microtom HM 360; Zeiss), using glass knives and contact cement at the lower cutting edge (HENRY 1977) to receive ribboned serial sections. The sections were stained with methylene blue-azure II (see RICHARDSON et al. 1960). Computer based 3D reconstruction of the female genital system was performed with the software AMIRA 3.0 (TGS Template Graphics Software, Inc., USA). The section series was deposited in the Zoologische Staatssammlung München (ZSM), Mollusca Section (ZSM Mol 20041037). For morphological and anatomical comparison, serial sections and 3D reconstructions of five individuals of *P. milaschewitchii* from the Mediterranean were used (ZSM Mol 20060522-20060525).

3. RESULTS

3.1. External morphology and spicules

Our examined living Brazilian specimen used for structural analysis, showed the usual body shape of marine interstitial acochlidians, with a cylindrical anterior head-foot complex that is completely retractable into a broadened and elongated visceral hump. The crawling individual measured approximately 2 mm, but the visceral hump was damaged. The overall body coloration was whitish, with the brownish digestive gland shining through the tissue. The oral tentacles were bow-shaped and curved, rhinophores were lacking (see Fig. 3A). The ciliated foot was short, i.e. there was no free tail extending behind the head-foot complex, and its posterior edge was rounded. Monoaxone (i.e. needle shaped) spicules (about 25 µm length) were found randomly distributed over the head-foot complex and visceral hump. Additionally, an accumulation of parallel orientated monoaxone spicules was detected between the oral tentacles. Light microscopic investigation of the sectioned head region indicates cilia on the anterior border of the head and oral tentacles.

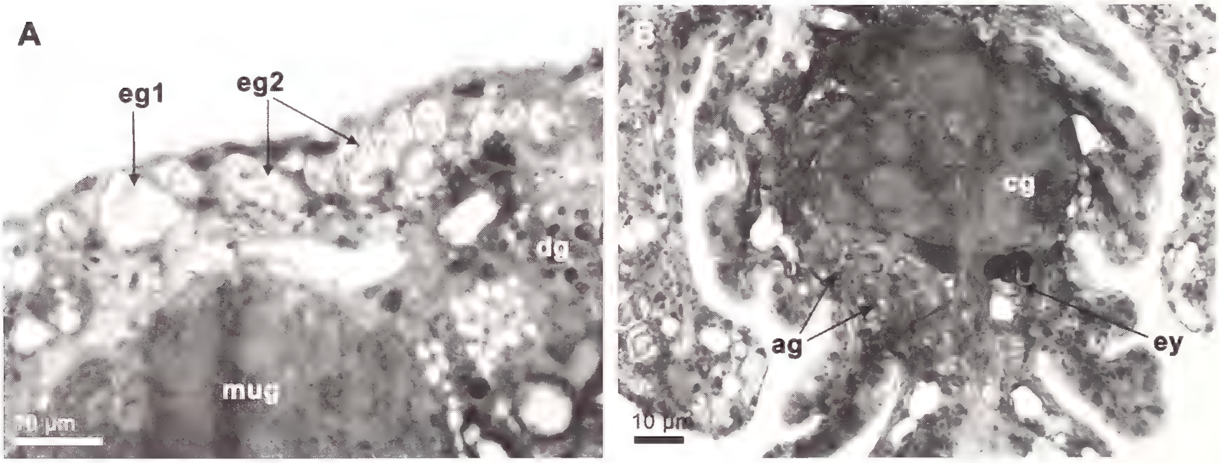

Fig. 1. Semithin sections of the female *Pontohedyle* from Brazil. (A) Cross-section of the visceral hump, showing the epidermis and the epidermal gland cells. (B) Horizontal section of the central nervous system. Abbreviations: ag accessory ganglia, cg cerebral ganglia, dg digestive gland, eg1 epidermal gland type I, eg2 epidermal gland type II, ey eyes, mug mucous gland.

3.2. Microanatomy

The bad condition of the only Brazilian specimen available for structural analysis did not allow detailed histological investigations of all major organ systems. Nevertheless, a brief treatise is given on the recognisable organs, focusing on the female genital system which could be reconstructed from serial sections.

3.2.1. Epidermal glands

The epidermis contains large spherical glandular cells (5-10 µm in diameter). They form a sub-epidermal sac, which is more or less filled with a homogenous whitish secretion (= epidermal glands type I, see Fig. 1A). Smaller vacuoles could be detected in the epidermis containing pinkish to violet stained granular material. These vacuoles occur in large numbers (= epidermal glands type II, see Fig. 1A).

3.2.2. Central nervous system

Praepharyngeal, large oval cerebral ganglia (approximately 50 µm), smaller pedal ganglia (approximately 30 µm) and groups of accessory ganglia could be detected. The cerebral ganglia are connected by a very strong and short commissure. A pair of dark pigmented eyes (diameter about 12 µm) nestles on the anterior side of the cerebral ganglia (see Fig. 1B). Groups of accessory ganglia are located anteriorly and laterally of the cerebral ganglia. Different from true ganglia true ganglia, accessory ganglia are well defined cell groups with a homogenous distribution of nuclei and without subdivision into cortex and medulla (NEUSSER et al. 2006). Here the accessory ganglia are more or less spherically shaped and grouped together like pearls on a chain (Fig. 1B).

3.2.3. Digestive system

The mouth opening is located subterminally between the oral tentacles. The thin walled oral tube is collapsed. The muscular pharynx extends in the posterodorsal part of the head-foot complex and contains the radula in its posterior region. The salivary glands form one mass on the left side of the head-foot complex, slightly extending into the visceral sac. The cells of the salivary glands contain dark blue stained granules. The tube-like oesophagus leaves the pharynx posterodorsally and connects to the digestive gland in the anterior region of the visceral hump. There is no histologically or anatomically detectable stomach. The digestive gland extends over the length of the remaining visceral hump and extrudes through the ruptured epidermis. It is sac-like in shape and its cells contain small dark blue and red stained granules. The epithelium of the digestive gland bears a series of small whitish and oval vacuoles. Neither the intestine nor the anal opening could be detected due to the bad condition of the animal.

3.2.4. Excretory and circulatory systems

Only the kidney could be detected. It is triangular in shape and squeezed in between the digestive gland and the body wall on the right side of the anterior region of the visceral hump. The epithelium of the kidney is characterized by its usual vacuolated structure.

3.2.5. Female genital system

The examined individual is a mature female, recognisable by the presence of vitellogenic oocytes in the ovary. The female genital system is composed of the ovary, the nidamental glands and the oviduct (Fig. 2A, B). The ovary extruded through the ruptured epidermis of the visceral sac and was partially falling apart. Nevertheless, seven large vitellogenic oocytes are still *in situ* (Fig. 2F). The oocytes are comprised of a nucleus containing one nucleolus and yolk (characterised by dense aggregations of blue stained granules). The oocytes reach a diameter of about 50–60 µm. The albumen gland is tube-like in shape and its secretory cells are stained dark blue to dark violet (Fig. 2E). The secretory cells are alternated by supporting cells, which bear cilia. The membrane gland is comparably large and tube-like in shape. Its secretory cells are stained pinkish with glandular appearance and containing vacuoles (Fig. 2D). The supporting cells bear cilia. The long tube-like mucous gland runs parallel to the digestive gland in the anterior region of the visceral sac. The supporting cells of the mucous gland are also ciliated and the secretory cells are stained dark violet. The three nidamental glands connect directly to each other (i.e. without any defined proximal oviduct or adhesive region, see Fig. 2A). The distal ciliated oviduct (Fig. 2C) ventrally passes the digestive gland and leads to the right anterior region of the visceral hump. The genital opening is located on the right side of the body, at the transition from the head-foot complex to the visceral hump. A short ciliated band originates at the genital opening. It has a diameter of about 10 µm and runs anteriorly along the right side of the head-foot complex.

4. DISCUSSION

According to WAWRA (1987), acochlidians belonging to the genus *Pontohedyle* share microhedylid features such as having separate sexes and lacking copulatory organs. *Pontohedyle* species were characterized by the absence of rhinophores and a radula formula of 1.1.1. The combination of these features is unique among acochlidians, but may refer to plesiomorphies. The special shape of

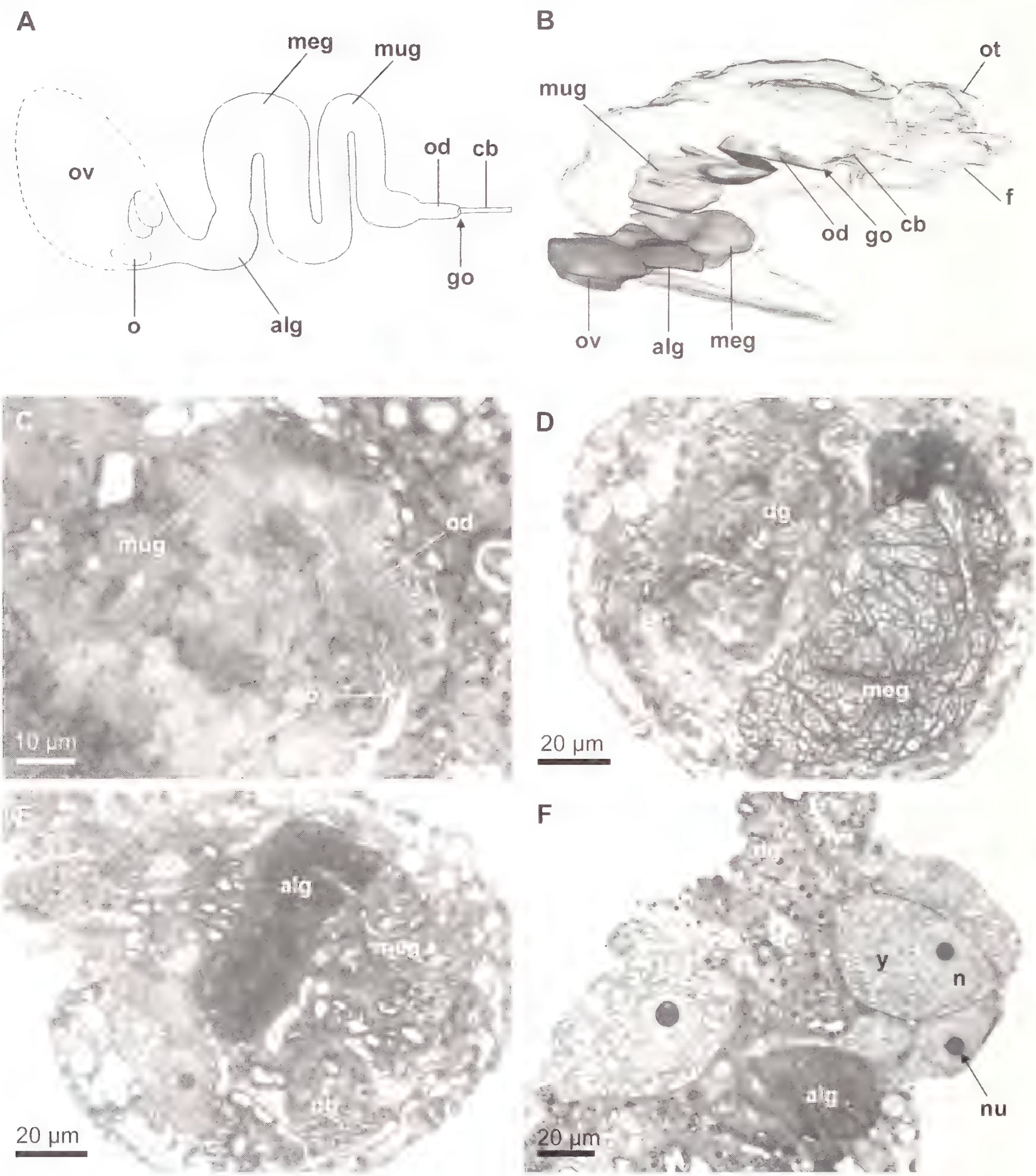
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Fig. 2. Female genital system of the *Pontohedyle* from Brazil. (A) Schematic overview, lateral view. (B) 3D reconstruction, lateral right view, specimen retracted, approximately posterior half of visceral sac and gonad missing (ruptured and therefore not reconstructed). (C) Semithin cross-section of oviduct and genital opening. (D) Semithin cross-section of membrane gland. (E) Semithin cross-section of the transition from albumen gland to membrane gland. (F) Semithin cross-section of mature oocytes. Abbreviations: alg albumen gland, cb ciliary band, dg digestive gland, f foot, go genital opening, meg membrane gland, mug mucous gland, n nucleus, nu nucleolus, o oocyte, od oviduct, ot oral tentacle, ov ovary, y yolk.

acochlidian oral tentacles may provide more phylogenetic information. Apart from species of the genus *Pontohedyle,* flat oral tentacles only occur in the genera *Hedylopsis* and *Ganitus.* While the oral tentacles of the *Hedylopsis* are much broader than those of *Pontohedyle* (see Fig. 3F), the ones of *Ganitus* appear similar. *Ganitus* can be differentiated since the oral tentacles are never tapered towards the end (see Fig. 3E). In fact, the flat, elongated to bow-shaped oral tentacles of *Pontohedyle*, which are tapered towards the end (see Fig. 3A-D), are unique and diagnostic, and thus, a probable autapomorphy of *Pontohedyle*.

WAWRA (1987) regarded two *Pontohedyle* species as being valid, the tropical Indopacific *P. verrucosa* (Challis, 1970) and the temperate *P. milaschewitchii* (Kowalevsky, 1901). RANKIN (1979) however, established an additional species *P. brasilensis* on the basis of a literature description of a single male specimen from Brazil. Table 1 compares potential distinguishing features of all three nominal *Pontohedyle* species, including the results of the present study on the female Brazilian specimen and the specimens of *P. milaschewitchii* from the Mediterranean used for comparison.

4.1. External morphology and spicules

Externally, the investigated specimen from Brazil confirms with the general acochlidian characters (e.g. visceral hump in which the head-foot complex can be at least partially retracted; see WAWRA 1987) and those of the genus *Pontohedyle* (lack of rhinophores). Using external characters, RANKIN (1979) differentiated *P. brasilensis* from *P. milaschewitchii* by referring to the flat triangular versus bow-shaped oral tentacles, and the absence or presence of cilia on head and oral tentacles. However, the shape of the oral tentacles is variable within specimens of Mediterranean *P. milaschewitchii* (see JÖRGER et al. in press). They vary from bow-shaped to elongated triangular, including the flat and triangular form described by MARCUS & MARCUS (1954) for the Brazilian specimen (see Fig. 3B). Already MARCUS & MARCUS (1954) illustrated that the tentacles can have a more rounded tip (see fig. 13, 14). This character clearly varies for one individual, depending on the contraction of the animal (see Fig. 3D: *P. verrucosa* with supposedly slightly retracted tentacles). The variability of this character between individuals is underlined by the observation of our northern Brazilian specimen that had bow-shaped oral tentacles in living condition (see Fig. 3A).

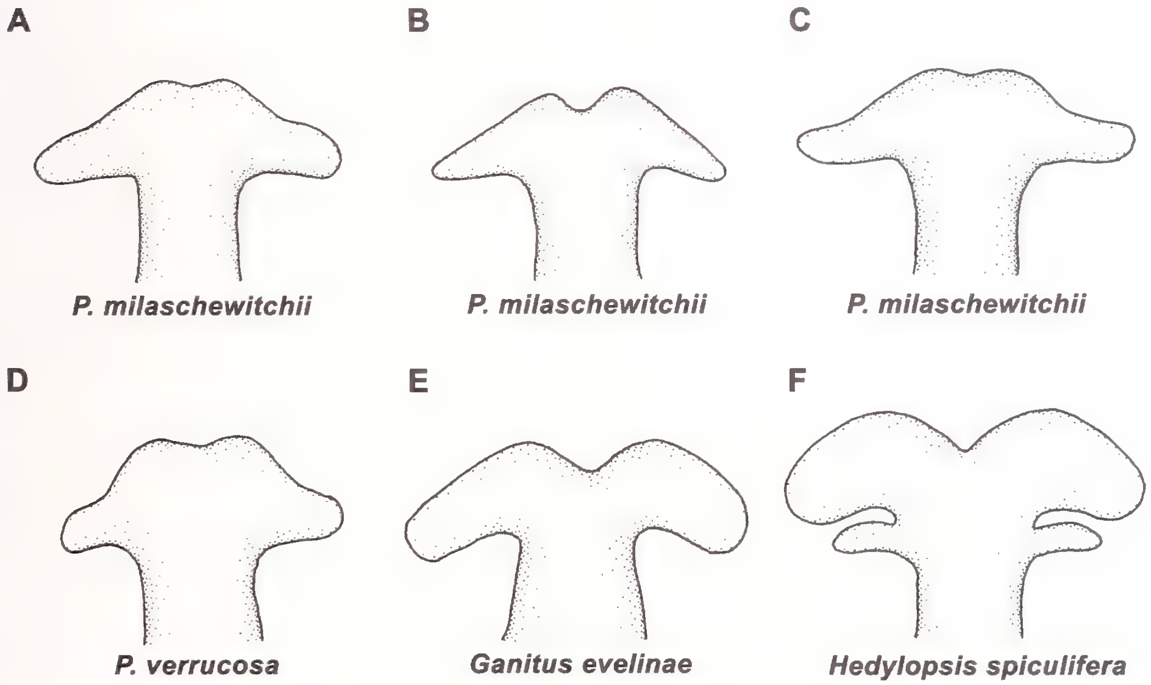

Fig. 3. Different types of flattened oral tentacles in acochlidians. (A) *Pontohedyle* from northern Brazil (present study), as *P. milaschewitchii.* (B) *P. milaschewitchii* from southern Brazil after MARCUS & MARCUS (1954; fig. 10). (C) *P. milaschewitchii* from the Mediterranean after KOWALEVSKY (1901; fig. 46). (D) *P. verrucosa* after CHALLIS (1970; fig. 5A). (E) *Ganitus evelinae* after MARCUS & MARCUS (1954; fig. 19). (F) *Hedylopsis spiculifera* (juvenile) after KOWALEVSKY (1901; fig. 49).

Table 1 . Comparison of characters previously used for species delineation in the genus *Pontohedyle*. ? = no data available; * Marcus & Marcus (1954) originally described the radula as 44 (2.1.2) misinterpreting the central denticle of the lateral plate as incomplete cleavage (Challis 1970; Jörger et al. in press).

	***P. milaschewitchii* (Kowalevsky, 1901)**	***P. brasilensis* (Rankin, 1979)**	***P. verrucosa* (Challis, 1970)**
Data source	Kowalevsky (1901) Wawra (1986) Jörger et al. (in press)	Marcus & Marcus (1954) present study	Challis (1970)
Collecting site	Sebastopol (Black Sea) Princess Islands, Lesbos Island, Istria (Mediterranean Sea)	São Paulo, Porto de Galinhas, Brazil (Atlantic Ocean)	Maraunibina Island, Solomon Islands (Pacific Ocean)
Collecting habitat	coarse and fine sands, sublittoral (2–9m)	coarse and shell sands, intertidal and 20m depth	coarse, shell sand, intertidal
Foot	very short, posterior tip rounded	very short, posterior tip rounded	very short, posterior tip free and pointed
Oral tentacles	bow-shaped to triangular/elongated	bow-shaped to triangular/elongated	bow-shaped
Spicules	- aggregation of needle-shaped parallel orientated spicules between the tentacles - randomly distributed needle-shaped spicules throughout the body	- aggregation of needle-shaped parallel orientated spicules between the tentacles - randomly distributed needle-shaped spicules throughout the body	absent (?)
Eyes	present	present	absent
Radula	- 41–54 (1.1.1) - rhachidian tooth with 1 central cusp and 3 lateral denticles - lateral plate with 1 central denticle	- 44 (1.1.1)* - rhachidian tooth with 1 central cusp and 3 lateral denticles - lateral plate with 1 central denticle	- 43 (1.1.1) - rhachidian tooth with 1 central cusp and 3 lateral denticles - lateral plate without denticle
Digestive system	- no stomach detectable - salivary glands form one mass on the left side of the body, discharging into the oesophagus close to the transition of the pharynx	- "large, spherical stomach" according to Marcus & Marcus (1954), but no stomach detectable in the present study - salivary glands form one mass on the left side of the body	- no stomach described - salivary glands paired, discharging into the oesophagus "near its posterior end"
Male genital system	ciliated vas deferens, extending to the level anterior to the oral tentacles, genital opening dorsal to the mouth opening	genital opening on the posterior end of the head-foot complex	?
Female genital system	ciliary band extending from the genital pore to about one third of the head-food complex	short ciliary band extending from the genital pore (present study)	?

RANKIN (1979) claimed cilia to be absent from the head and oral tentacles of *P. milaschewitchii,* in contrast to *P. brasilensis*. However, a constant pattern of cilia could be detected on the oral tentacles of Mediterranean *P. milaschewitchii* (see JÖRGER et al. in press). Similar cilia were described for the Brazilian specimen by MARCUS & MARCUS (1954) and were also observed for the northern Brazilian specimen herein. Therefore, these external characters cannot be further used for separating species. In contrast, the Brazilian specimen described by MARCUS & MARCUS (1954) and the one studied herein resemble specimens of *P. milaschewitchii* (see JÖRGER et al. in press; KOWALEVSKY 1901) in all examined details, e.g. 1) body size and coloration, 2) shape of oral tentacles, 3) foot (short, posterior end rounded), 4) type (monoaxone) and position (accumulation between oral tentacles and randomly distributed all over the body) of spicules, and 4) presence of cilia on head and oral tentacles.

4.2. Microanatomy

Anatomically, RANKIN (1979) saw differences between *P. milaschewitchii* and *P. brasilensis* regarding fused versus separated cerebral and pleural ganglia, the radula formula, the presence/absence of a well developed stomach, and the development of the salivary glands.

4.2.1. Central nervous system

Probably based on small semi-schematic drawings of an entire specimen of *P. milaschewitchii* by KOWALEVSKY (1901; fig. 46, 48), RANKIN (1979) claimed the cerebral ganglia to be fused with the pleural ganglia in *P. milaschewitchii,* while they were described to be separated in *P. brasilensis*. We could not clearly detect pleural ganglia in our damaged northern Brazilian specimen. However, JÖRGER et al. (in press) showed that the cerebral and pleural ganglia in Mediterranean *P. milaschewitchii* specimens are clearly separated, as usual for Acochlidia (HUBER 1993; SOMMERFELDT & SCHRÖDL 2005; WAWRA 1987).

4.2.2. Digestive system

MARCUS & MARCUS (1954) described a radula formula of 44 x 2.1.2 for their Brazilian specimen. However, CHALLIS (1970) suggested that the denticle in the lateral tooth might have been misinterpreted as a gap that appears to separate one broad lateral tooth into two. This explanation was accepted by WAWRA (1987) and is indeed very convincing. The radula of Mediterranean *P. milaschewitchii* closely resembles the one described by MARCUS & MARCUS (1954) for the Brazilian specimen: there is a triangular rhachidian tooth with one central cusp that is bordered by three lateral denticles, and just one broad lateral plate on each side with one central denticle, thus with the formula 1.1.1 (JÖRGER et al. in press).

MARCUS & MARCUS (1954) saw an unusual large, spherical stomach in their Brazilian specimen, which was reflected in Rankin's generic name *Gastrohedyle*. No special stomach was detected in our Brazilian specimen, but an oesophagus passing into a moderately developed digestive gland cavity which was filled with particles. This reflects the normal condition found in Mediterranean *P. milaschewitchii* (see JÖRGER et al. in press), and all other marine acochlidians. The large "stomach" described by MARCUS & MARCUS (1954) maybe easily explained as referring to a digestive gland cavity filled with particles or artificially swollen by gases due to decomposition.

RANKIN (1979) declared the salivary glands of *P. milaschewitchii* as "paired, well separated, long, thin, and tapering" in contrast to the large spherical salivary glands of *P. brasilensis* forming one mass on the left side of the body. However, the salivary glands in Mediterranean *P. milaschewitchii* are just like those described by MARCUS & MARCUS (1954) for the Brazilian specimen and also those observed herein (JÖRGER et al. in press).

4.2.3. Genital system

MARCUS & MARCUS (1954) described their male Brazilian specimen as having a genital opening located on the right side of the head-foot complex close to the transition to the visceral hump. This is the usual position for the female genital pore *P. milaschewitchii* and of other male and female genital pores in microhedylid acochlidians. However, Mediterranean male *P. milaschewitchii* show a male genital pore in an unusual cephalic position dorsal to the mouth opening (JÖRGER et al. in press; WAWRA 1986). MARCUS & MARCUS (1954) used the anterior part of the head-foot complex of their specimen for radula preparation and were therefore unable to detect a male genital opening in an anterior position. The putative posterior opening in the male Brazilian specimen maybe thus explained by generalization and misinterpretation or maybe due to different ontogenetic stages. If additional male Brazilian specimens in different ontogenetic stages did not show any ciliated duct leading anterior to a cephalic male genital opening but a posterior genital opening, this would be the first serious indication for a specific separation of *P. brasilensis* from *P. milaschewitchii*.

The female genital system of our Brazilian specimen closely resembles the one observed for *P. milaschewitchii* (JÖRGER et al. in press; WAWRA 1986) in 1) presence of a ciliary band originating from the genital opening; 2) position of the genital opening; 3) development and histology of the nidamental glands; 4) comparably small size of mature oocytes (around 60 µm). No differentiating features between the Brazilian specimen and its Mediterranean counterparts could be detected concerning the female genital system.

4.3. Taxonomy

All the differences between *P. milaschewitchii* and *P. brasilensis* claimed by Rankin (1979) are non existent (cilia pattern, radula formula, shape of salivary glands, fusion of cerebral and pleural ganglia), variable (shape of oral tentacles) or can be easily explained by biological factors and artefacts (presence of large "stomach"). Morphological knowledge available at present (Table 1) strongly supports Wawra (1987) in considering *P. brasilensis* as a junior synonym of *P. milaschewitchii*. However, the considerable geographical distance between the Mediterranean and the northern and southern Brazilian populations of an interstitial species and the hydrographic differences between warm temperate and tropical waters require molecular investigation as soon as abundant Brazilian populations can be found.

Pontohedyle milaschewitchii as defined above is a Mediterranean and Atlantic species, while *P. verrucosa* was described from the Solomon Islands in the tropical Indopacific (Challis 1970). Main differences to *P. milaschewitchii* are the absence of spicules, eyes and lateral radula denticles (Table 1). However, at least the lack of spicules might be due to a preservation artefact; *P. verrucosa* urgently needs redescription and comparison with some other potentially undescribed *Pontohedyle* species found in the tropical Indopacific (see Schrödl et al. 2003).

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Pleurobranchaea inconspicua Bergh, 1897 (Opisthobranchia: Pleurobranchidae): Redescription and distribution from Argentina and Colombia*

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Abstract. A taxonomic study based on fresh specimens from Argentina and Colombia, and voucher material from the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN) and Museo de Historia Natural Marina de Colombia (MHNMC-INVEMAR) was conducted. The first study by scanning electron microscopy (SEM) of the radular, jaw elements and reproductive anatomy, paying special attention to the internal cuticular stylet of the penis, is presented. Previous descriptions of *P. inconspicua* and its junior synonyms, *P. hamva, P. hedgpethi*, and *P. gela*, are compared with the present results; *P. bonnieae* is synonymized and a checklist of the distinguishing features of relevant species within the genus *Pleurobranchaea* is provided. This work aims at discussing the proposed amphiatlantic distribution of *P. inconspicua* and at solving the problems of synonymies. It provides a starting point for a comparative study of specimens of the genus *Pleurobranchaea* from both sides of the Atlantic Ocean and the Mediterranean Sea that will be complemented with molecular studies in future times.

Keywords. Taxonomic redescription, Colombian Caribbean, Argentina, amphiatlantic distribution.

1. INTRODUCTION

The genus *Pleurobranchaea* Meckel in Leue, 1813 is represented in temperate-warm waters, by several species with wide geographical distribution ranges. *Pleurobranchaea inconspicua* Bergh, 1897 was described from northern Brazil (type locality: Sergipe, 10° 54´S, 37° 7´W), and its distribution was later extended under the same name or under junior synonyms of species and subspecies to several localities in the Western Atlantic Ocean (USA, Caribbean, Brazil, Argentina) and to localities more distant from the type locality, such as the Mediterranean Sea (Israel) and West Africa (Ivory Coast to Nigeria).

Marcus & Gosliner (1984) gave the most recent revision of the subfamily Pleurobranchaeinae, which included 14 species of the genus *Pleurobranchaea*. However, these authors did not include the species *P. morosa* Bergh, 1892, *P. morula* Bergh, 1905, *P. melanopus* Bergh, 1907, *P. algoensis* Thiele, 1925, *P. japonica* Thiele, 1925, and *P. dorsali* Allan, 1933, because they were poorly described. Nevertheless, *P. japonica* was redescribed by Tsubokawa et al. (1992), confirming the validity of the species and *P. morosa* has been recently mentioned from Azorean archipelago by Malaquías (2001) and Cervera et al. (2006), although both works refer to the original description only.

In Marcus & Gosliner's revision (1984), the names *P. hedgpethi* Abbott, 1952, *P. hamva* Marcus and Marcus, 1955 (mispelled *hamwa*) and *P. gela* Marcus and Marcus, 1966 were considered junior synonyms of *P. inconspicua*. Abbott (1952) described *P. hedgpethi* from Port Aransas (Gulf of Mexico); this species became the most frequently mentioned junior synonym of *P. inconspicua* for the Western Atlantic, even more frequently than the senior synonym. However, in the same revision, these authors erected the species *P. bonnieae* for one specimen from Florida region. According to Valdes et al. (2006) this name could be another junior synonym of *P. inconspicua*.

Several authors considered the anatomy of the reproductive system and the penial morphology as the most useful characters to discriminate species of the genus *Pleurobranchaea* compared to the classical hard structures of radulae and jaws (Marcus 1961; Marcus & Gosliner 1984; Willan 1987).

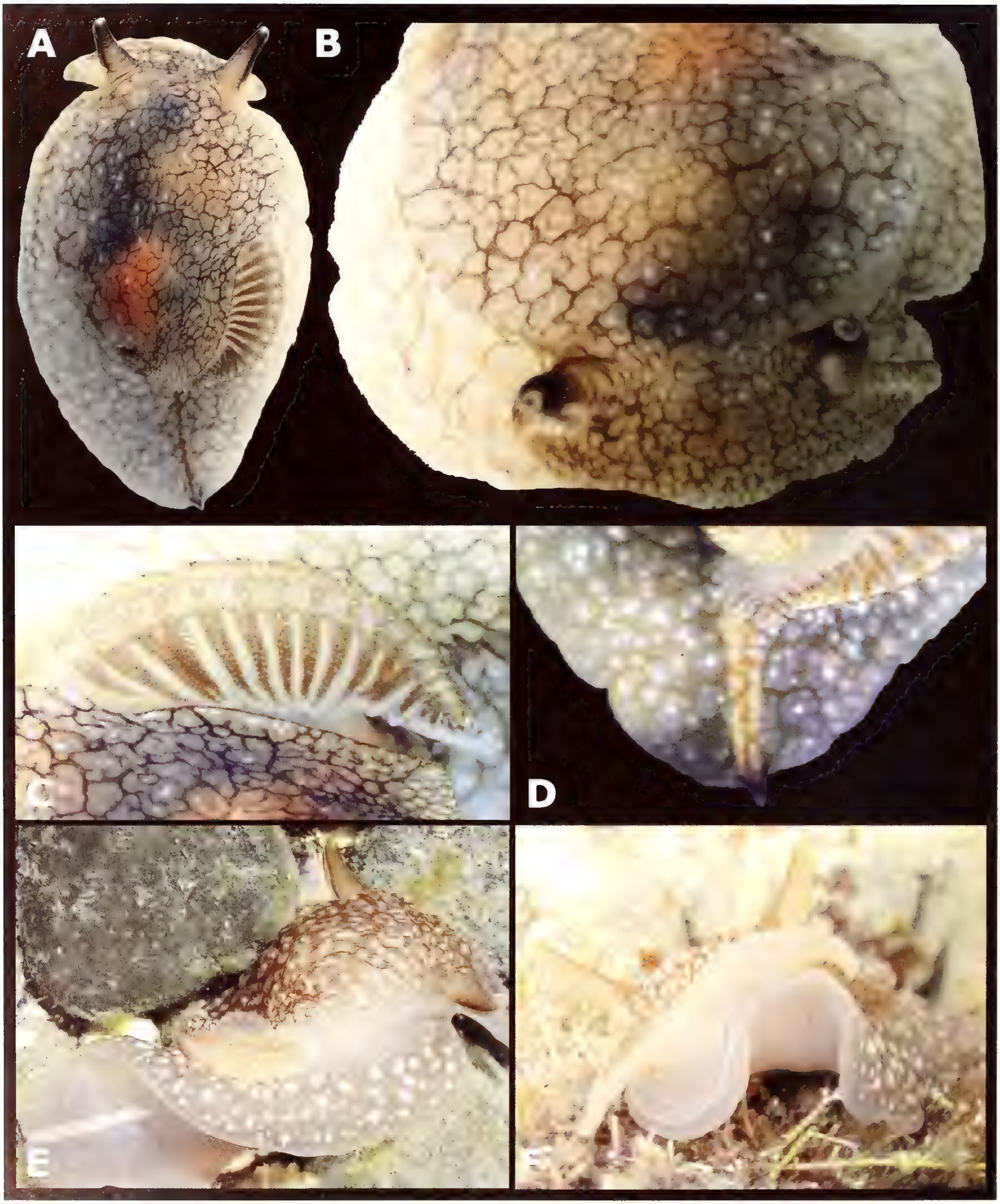

Fig. 1. *Pleurobranchaea inconspicua* Bergh 1897. A. Dorsal view of living specimen from Colombia (Photo: N. Ardila). B. Dorsal view of head. C. Detail of the gill and the pairs of pinnules. D. Foot showing a conspicuous spur. E. Living specimen from Patagonia (80 mm length) (Photo: C. Muniain). F. Detail of rhinophores and sensory papillae on the oral veil (Photo. C. Muniain).

Unlike most of the previous descriptions of *P. inconspicua* and of other species of the genus conducted from preserved material, often in bad conditions, this work redescribes the characteristics of recently collected specimens of *P. inconspicua* from two distant localities.

This is the first study using SEM for hard structures of *P. inconspicua*, especially the examination of the penial stylet. Detailed descriptions of the external appearance and the hard structures, as well as the reproductive system, of specimens from distant localities help to understand the intraspecific variability in this species, and allow to discuss the possible amphiatlantic distribution of *P. inconspicua* by comparison with material from other Atlantic localities. Here, synonymization of other *Pleurobranchaea* species with *P. inconspicua* is outlined.

2. MATERIALS AND METHODS

Specimens were collected over a wide range of depths from shallow intertidal areas down to 150 m in depth. A total of 16 specimens were preserved in 70% ethanol. Photographs and videos were obtained with a digital camera from living specimens. Part of this material is deposited in the Museo de Historia Natural Marina de Colombia (MHNMC-INVEMAR) as well as in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN).

Colombia: Four specimens collected with a bottom trawl (9 x 1 m opening, 16 m in length) during the research cruises INVEMAR-MACROFAUNA II, 2001 aboard the R/V Ancon, in the Caribbean coast of Colombia at 70 and 150 m depth; two specimens off Dibulla (11° 25' 34"N, 73° 27' 40"W), E-100, 150 m depth (MHNMC-INVEMAR: 3872, 3873), two specimens off Buritaca (11° 18' 28"N, 73° 46' 50"W) E-108, 109, 70 m depth (MHNMC-INVEMAR: 3874, 3875). One specimen was collected by SCUBA from Neguanje Bay, 5-10 m depth in a culture of bivalves (Ardila priv. coll.).

Argentina: One specimen from Puerto Quequén (38° 34`S, 58° 38`W) Buenos Aires, 12/1928, MACN-in: 18234; one specimen from Puerto Quequén, Buenos Aires, 2/1929, MACN-in: 18312; two specimens from Puerto Quequén, Buenos Aires, 1/1934, MACN-in: 412; six specimens from Creek Bay (41° 6`S, 63° 56`W), San Matías Gulf, Río Negro, MACN-in: 36985; one specimen from Larralde (42° 25`S, 64° 19`O), San José Gulf, Chubut, 10/1/2006, MACN-in: 37064.

Two specimens were dissected, and their jaws and radulae were removed and mounted for Scanning Electron Microscopy (SEM) examination (MACN-in: 36985, 37064). Two penises and their respective cuticular stylets were previously critical-point-dried for SEM (MACN-in: 36985, 37064).

3. RESULTS

3.1. Systematic description

Nudipleura Wägele & Willan, 2000
Pleurobranchoidea Gray, 1827
Pleurobranchidae Gray, 1827
Pleurobranchaeinae Pilsbry, 1896
Pleurobranchaea Meckel in Leue, 1813 (type *Pleurobranchidium meckelii* Blainville, 1826)

***Pleurobranchaea inconspicua* Bergh, 1897** (Figs 1–5)

Pleurobranchaea inconspicua Bergh, 1897 (Bergh 1897: 49-51, pl. 8, figs 2–10. Marcus & Gosliner 1984: 24–27, figs 1B, 10–11. Ríos 1984: 206–207, pl. 69, fig. 987. Muniain 1997: 4, 17, 34. Ardila & Rachello 2004: 62, fig.3).

Pleurobranchaea hedgpethi Abbott, 1952 (Abbott 1952: 1–2, pl. 1, figs 1–8. Marcus & Marcus 1959: 253 fig. 6. Marcus & Marcus 1960: 253–254, fig. 6. Nijssen-Meyer 1965: 143–145, figs 1–2. Marcus & Marcus 1967a: fig. 55C. Marcus & Marcus 1967b: 200. Marcus & Marcus 1969: 18. Abott 1974: 348, fig. 4201.

Pleurobranchaea hamva Marcus & Marcus, 1957 (Marcus & Marcus 1957: 21–27, figs 40–52).

Pleurobranchaea hedgpethi hamva Marcus, 1961 (Marcus Er. 1961: 141. Marcus & Marcus 1967a: 48).

Pleurobranchaea gela Marcus & Marcus, 1966 (Marcus & Marcus 1966: 174, figs 35–37.

Pleurobranchaea bonnieae Marcus & Gosliner, 1984 (Marcus & Gosliner 1984: 29–32, figs 1D, 13–14.).

3.1.1. External features

Length of the living animals ranges between 13 and 80 mm.The body is oval and elongate. The ground colour is pale cream, with a dense dark brown reticulate along the mantle dorsal region, being lighter and less obvious in the foot dorsal region and absent in the well developed rhinophores (Fig. 1A, B, E). Bright white spots are scattered all over the mantle and more conspicuous on the dorsal foot surface. The oral veil is broad with sensory papillae along the anterior edge. Rinophores are held erect in the living animals (Fig. 1B, F), whereas in the preserved ones they are in a lateral position.

The mantle is reduced and fused with the oral veil; a large gill is visible on the right side of the body. The gill is attached along most of the body with about 26 pairs of pinnules per gill (Fig. 1 C, E). The anal papilla lies over the seventh pinnule. The foot is rounded in front. The soft mantle, not covering the foot, is visible to most of its part (Fig. 1 A, E). The coloration in the ventral foot region is translucent, and the internal organs can be observed by transparency. At the posterior end, the foot ends in a rounded shape, with a large metapodial gland (yellowish) extending longitudinally from the posterior mantle towards the central foot sole (Fig. 1 E). Dorsally to the metapodial gland, the foot has a brown or black tiny spur (Fig. 1A, D).

3.1.2. Anatomy

A shell is lacking. The pharyngeal bulb frequently protruded in preserved specimens through the eversion of the very extensible oral tube. Jaws consist of two paired and elongate chitinous plates on the lateral walls of the pharyngeal bulb. The radular formula of one specimen of 40 mm in life is 30 X 64.0.64 (MACN-in: 36985). The radula lacks a rachidian tooth, but a difference among the first four laterals is noticeable in some radular rows (Fig. 2A). Lateral teeth are bicuspid, largest in the middle of the half-row and smaller towards the outer border (Fig. 2B). The jaw elements (rodlets) bear 4 to 8 denticles from the outermost and innermost region (Figs 2C, D).

The reproductive system arrangement is similar to that of other *Pleurobranchaea* species (Fig. 3). The tubular ampulla forks near its outlet into two branches, the shorter branch is the oviduct that enters the capsule gland, and the other branch is the efferent duct that splits in two. One branch enters the prostate and then continues within the penial sac (Fig. 3, number 4). The second branch leads to the bilobed seminal receptacle, which is connected to the bursa copulatrix by a long and thin convoluted duct. The bursa copulatrix is large and round.

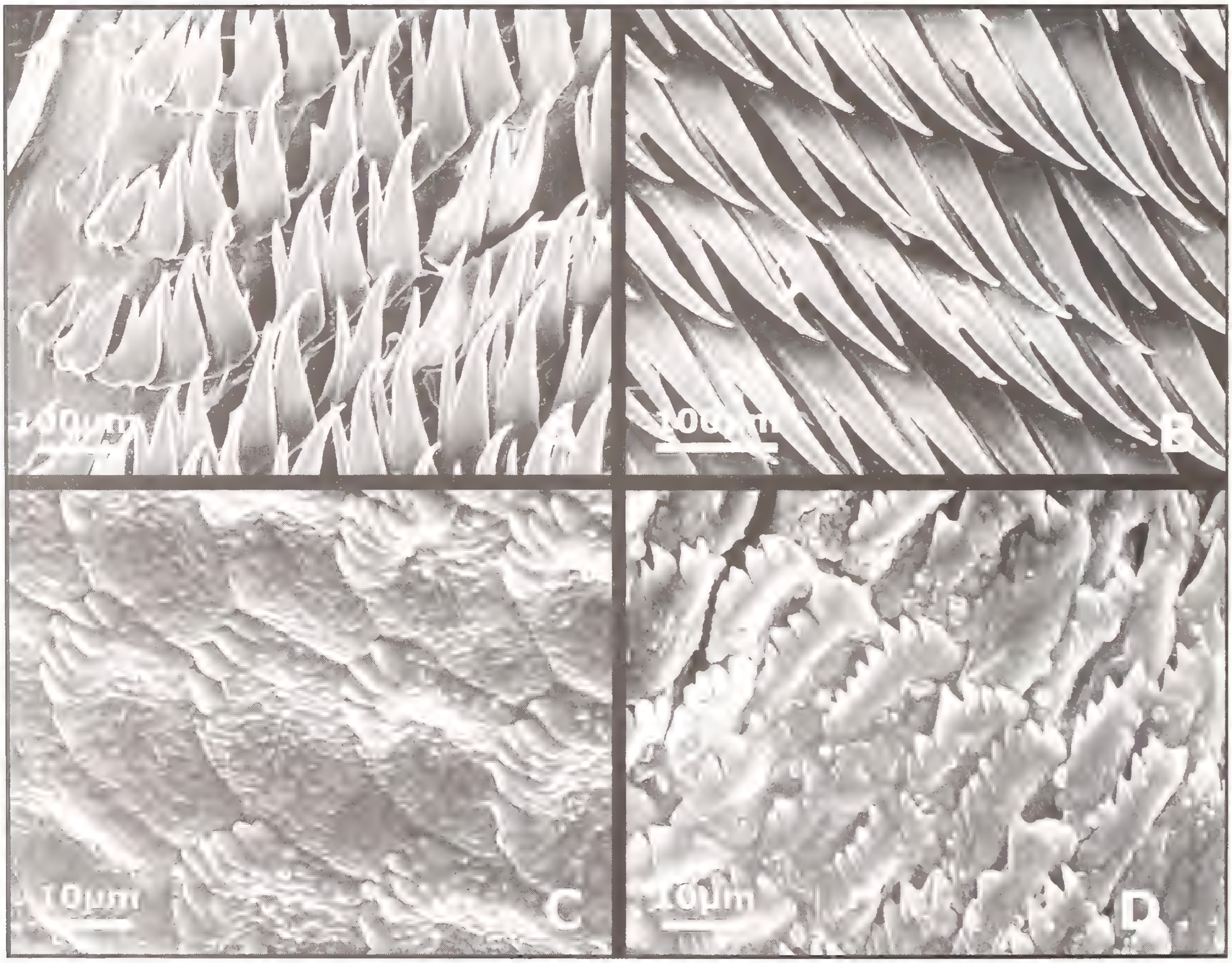

Fig. 2. A–D. Scanning electron photographs of radula of *P. inconspicua* MACN-in: 36985. A. Radula lacking a rachidian central tooth. B. Outermost teeth on the same radula side (right). C, D. Jaw showing platelets with 4–8 denticles from outermost region. D, Jaw showing platelets from innermost region.

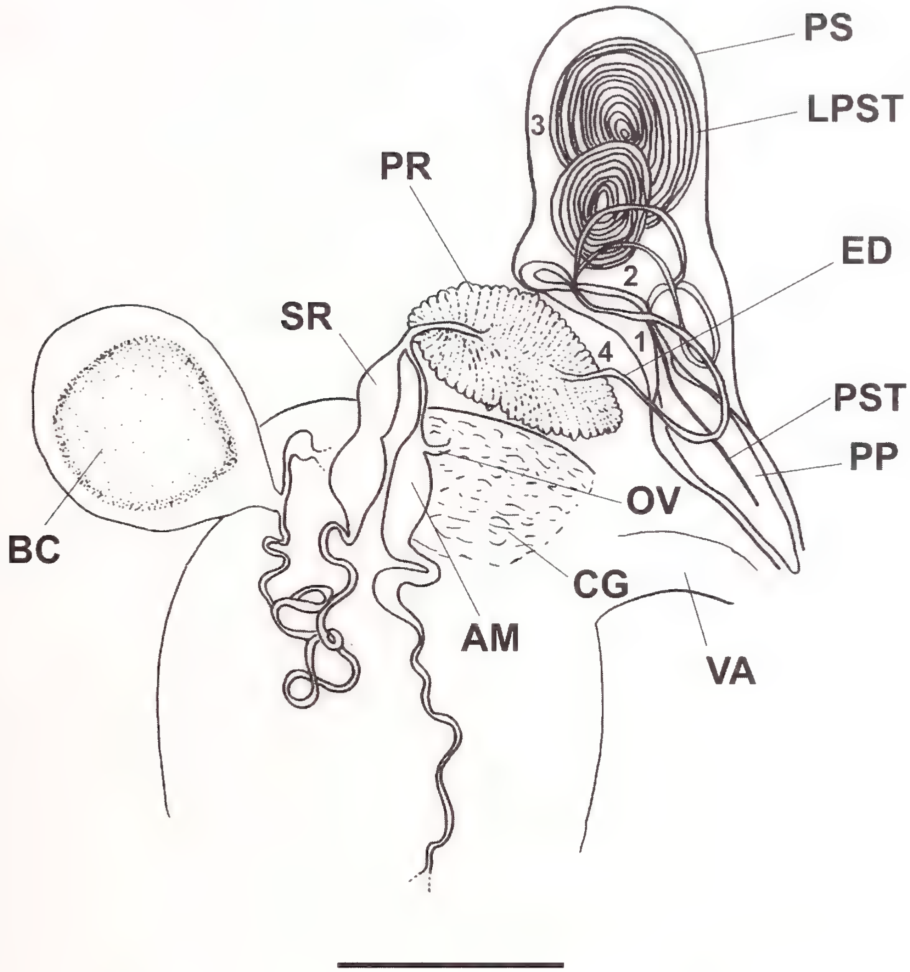

Fig. 3. Reproductive system of *P. inconspicua* MACN-in: 36985. Scale bar: 1mm. Abbreviations: AM ampulla, BC bursa copulatrix, CG capsule gland, ED efferent duct, LPST penis loop containing the cuticular stylet, OV oviduct, PP penial papilla, PR prostate, PS penial sac, PST penis (cuticular stylet), SR seminal receptacle, VA vagina. For numbers see text.

The penis is an elastic cutilar stylet, that coils in numerous helically loops (Fig. 3, number 3), that finally enters in the atrium through a penial papilla (Fig. 3, numbers 2, 1). It is difficult to find the point where the efferent duct and the penis are connected. When stretched out, the penis reaches a length of 16 and 20 cm in specimens of 45 and 80 mm length respectively. Observations of the penis under SEM reveal an external cuticule and internal cuticular stylet throughout its length (Fig. 4 A–E).

A transversal section of the penis shows that the chitinous stylet is not rounded and has a central cylindrical orifice. The shape and size of these penial stylets from two specimens examined under SEM are similar (Figs A, B, C). The width of those stylets is about 80 µm. The penis has more than 15 roundish loops (Fig.3, LPST, number 3), and contains the cuticular stylet all along its length (Fig. 4D). The penial stylet runs only along one fifth of the penial cuticule (Fig. 4E). Apparently, as observed from the detail of the final portion of the efferent duct, in its portion connecting with the prostate, a central cuticular stylet inside it would be lacking (Fig. 4F).

3.2. Geographic distribution

The geographical distribution cited for *P. inconspicua* is from Cape Hatteras, North Carolina 35° N 80° W (USA) to San José Gulf 42° S 64° W (Argentina) (See Table 1, Fig. 5). Regarding the Caribbean distribution of this species, the first record from Colombia was given by ARDILA & RACHELLO (2004), with specimens from 70-150 m and an individual collected from 8–10 m, present study.

MARCUS & MARCUS (1969) recorded specimens for the first time (as *P. hedgpethi*) for Argentina (40° 32` S, 60° 19` W, 19 specimens at 57 m) and (40° 11` S, 60° 27` W,

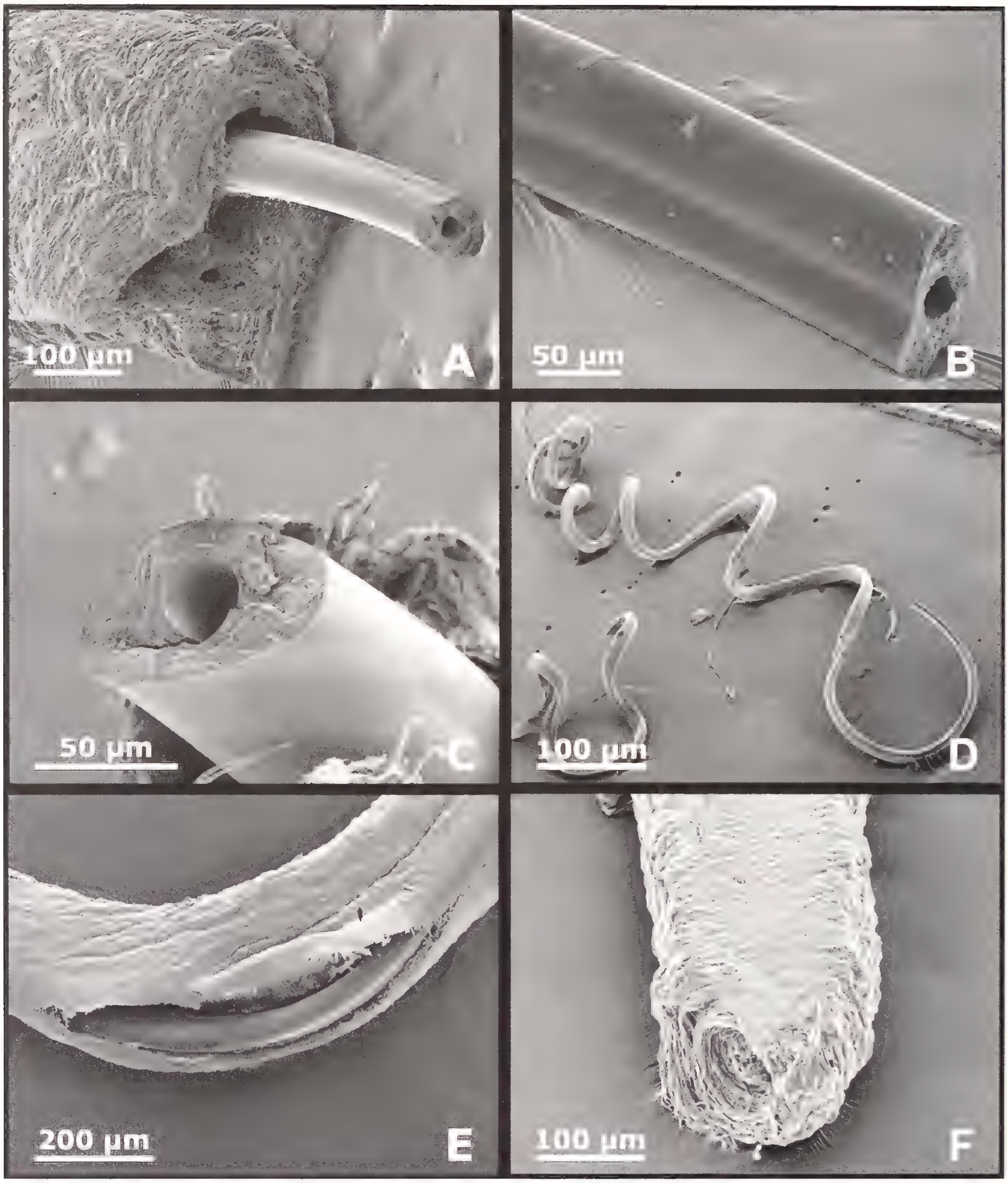

Fig. 4. SEM (critical-point-dried) of reproductive system of *P. inconspicua* (MACN-in: 36985; 37064). A. Penis, showing the external cuticule and internal chitinous stylet (MACN-in: 36985); B and C. Detail of the tranverse section of the cuticular stylet of two different specimens (B, MACN-in: 36985; C, MACN-in: 37064). D. Portion of penial loop with a length of 20 cm from specimen of 80 mm in length (MACN-in: 37064). E. Dorsal view of the external cuticule, showing a portion of the cuticular stylet inside it (MACN-in: 36985). F. Detail of the region of the efferent duct that leaves the prostata (MACN-in: 37064).

7 specimens at 44 m), and their geographical range has been extended to northern Patagonia some years later for the intertidal to 8 m (Muniain,1997, present study).

Marcus & Gosliner (1984) cited localities from the Mediterranean Sea (Israel) and West Africa (Ivory Coast to Nigeria). Further investigations will allow testing the hypothesis of an amphiatlantic distribution.

4. DISCUSSION

As mentioned above, this work intends to serve as a starting point for further taxonomic and molecular studies involving a larger number of fresh material to verify whether this species is also present along the western coasts of Africa and the eastern Mediterranean (Israel) (amphiatlantic species), as Marcus & Gosliner (1984) stated, or

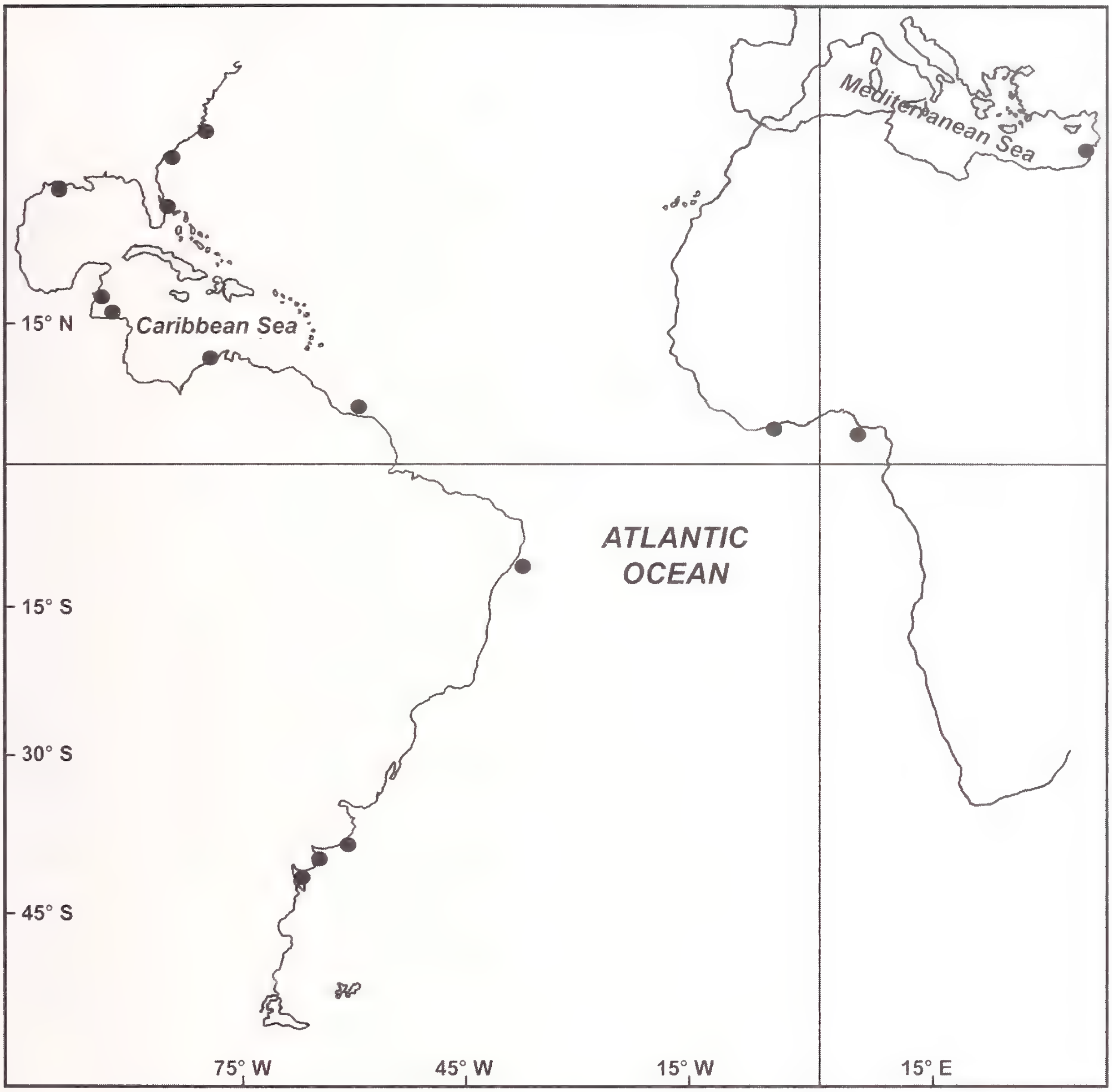

Fig. 5. Known distribution of *Pleurobranchaea inconspicua* Bergh, 1897, including its synonyms.

to confirm the validity of other species of the genus (e.g. *P. tarda* from Western and South Eastern Atlantic, Table 1, Fig. 5).

Thus, VALDÉS et al. (2006) suggest that *P. bonnieae* Marcus and Gosliner, 1984 could be a junior synonym of *P. inconspicua*. We agree with this opinion, since the description of this species is based on a single preserved and, very probably, juvenile specimen and the features suggested to differentiate it from other nominal species (*P. inconspicua* or *P. vayssierei*) are weak (presence of a penial cuticle or diameter of the base of the penis as they can be artifacts of preservation). There is no description of the living animal. Besides all the facts stated above, MARCUS & GOSLINER (1984) provide unclear information about the collecting localities of their material of *P. inconspicua*, but they give a geographical range in the western Atlantic that would include the type locality of *P. bonnieae*. Another species of *Pleurobranchaea*, *P. agassizi* Bergh, 1897, would fit the geographical range for *P. inconspicua*. However, the colour of living specimens of *P. agassizi*, its bathymetric range and some anatomical differences concerning the radular teeth and the reproductive system make us consider this species as valid until additional fresh material can be studied.

External and internal characteristics of *P. inconspicua* have been described from fresh collected specimens from two distant localities of its wide distribution, as well as from preserved material. The number of pinnae of the gill and the presence of a conspicuous caudal spur are shared by all dissected specimens. All Patagonian living specimens showed the caudal spur; but it is possible that after preservation the spur is not evident, and for this reason in some descriptions it might have not been mentioned. The same hypothesis can be drawn for the posterior region of the foot sole, in which a yellow metapodial gland forms a longitudinal furrow, often visible by transparency through the skin of the dorsal side of the tail. The internal anatomy, the radula, the jaw elements and the arrangement of the reproductive organs fully agree with previous descriptions. The morphology of the internal cuticular cylindrical stylet is similar to that illustrated by Marcus & Gosliner (1984, fig. 1B) by optical transverse section.

An updated review of the species of *Pleurobranchaea* with details of the radular and jaw elements using SEM is needed. Although at present these characters are not considered for specific identifications, they can provide further information that can be used in the comparison of species of dubious identity. Regarding the reproductive system, the presence of a penis with cuticular stylet is an important character to separate species, but its occurrence in many species is not clear, as in *P. californica*, MacFarland, 1966 and *P. meckelii* Meckel in Leue,1813. Some authors indicate its presence while others do not. Cervera & García-Gómez (1988) suggest that *P. notmec* Marcus and Gosliner, 1984 and *P. vayssierei* Marcus and Gosliner, 1984 are junior synonyms of *P. meckelii*, which agrees with a personal communication by Richard Willan. The *P. notmec*'s holotype is from eastern Mediterranean (off Turkey) but the paratypes are from Israel (Marcus & Gosliner 1984), as well as one specimen attributed to *P. inconspicua* by the same authors. On the other hand, *P. vayssierei* Marcus and Gosliner, 1984 was described from a single specimen from Algiers (Western Mediterranean) among the Vayssiere's material attributed to *P. meckelii*. The diagnostic features used to erect *P. notmec* and *P. vayssiere* seem weak to us since these species are described from few specimens and the characters vary intraspecifically (e.g. ontogeny) or could be artifacts due to preservation. Even Marcus & Gosliner (1984) overlooked, or were not able, to place *P. notmec* within their key to the species of Pleurobranchidae. Overall, we think that a final decision on the identity of this species will be possible only after a review of the type material and after additional fresh material is studied from the type localities areas based on both methods, morphological and molecular analyses. A future revision of type material of *P. notmec* and *P. vayssierei*, of further specimens from the type localities, as well as of *P. inconspicua* individuals from the Mediterranean Sea (Israel), will allow to elucidate the existence of more than one species of this genus in the Mediterranean or confirm that *P. meckelii* is the only species present in this region.

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Table 1. Diagnostic features of species of the genus *Pleurobranchaea* Leue, 1813.

Species	Geographical Distribution	Radular formula	Body Length (mm)	Cuticular stylet	Metapodial Spur	References
Pleurobranchaea meckelii (Blainville, 1825)	Type Locality: ? Mediterranean Other localities: Several Mediterranean localities (Naples, Sicily, Marseille, Genoa), Atlantic and Mediterranean Iberian Peninsula, Canary Islands, Azores Islands,Cape Verde Islands. 0–150 m.	46 X 71-0-71 50-60 X 65-55.1.55-65 ? X 70.1.70 ? X 70.0.70 40-50 X 60-70.0.70-60	up to 100	present	present	VAYSSIÈRE (1885, 1901, 1902) , BERGH (1897), MARCUS & GOSLINER (1984), CERVERA & GARCÍA-GÓMEZ (1988), CERVERA et al. (2006)
P. maculata (Quoy & Gaimard, 1832)	Type Locality: ? Southern Australia Other localities: Jarvis Bay (New South West, Australia), New Zealand, Japan ?, South Africa ?, Indo West Pacific. 0–300 m.	25 X 50-0-50 40-49 X 80-0-80 40-50 X 70-80.1.80-70	up to 50	No data	present	VAYSSIERE (1901), THOMPSON (1970), WILLAN (1983), MARCUS & GOSLINER, (1984), BURN (1989; 2006)
P. tarda Verril, 1880	Type Locality: ? Martha's Vineyard (Masschussets) Other localities: West Atlantic from Masschussets to south of Cuba. East Atlantic from Ghana & Cape of Good Hope, South Africa. 0–1450 m.	? X 70.0.70	7.5–110	present	present	VAYSSIERE (1901), MARCUS & GOSLINER (1984)
P. obesa (Verril, 1882)	Type Locality: ? 39°53´00´´N, 69°50´ 30´´W Other localities: East Coast of North America. 353–571 m.	34 X 90-0-90 38 X 80.0.80	40–128	present	present	BERGH (1897), VAYSSIÈRE (1901), MARCUS & GOSLINER (1984); GOSLINER (1985)
P. morosa (Bergh, 1892)	Type Locality: Strait of Pico-Fayal (Azores Islands). 130 m.	37 X 70-68.0.68-70	15	No data	No data	BERGH (1892), MALAQUÍAS (2001), CERVERA et al (2006)
P. agassizii Bergh, 1897	Type Locality: ? Straits of Florida, Great Bahama Bank (NW Atlantic), 200–620 m.	32 X 98.0.98 35 X 90.0.90	20	No data	present	BERGH (1897), VAYSSIÈRE (1901), MARCUS & GOSLINER (1984)
P. brockii Bergh, 1897	Type Locality: ? Amboine (Indian Ocean) Other localities: Indo West Pacific, Japan, Hong Kong, South Africa, Australia. 0–60 m.	40-48 X 65.90.0.65.90 36 X 58.0.58 52 X 52.0.52 35 X 65.0.65	38–110	No data	present	BERGH (1897), VAYSSIERE (1901), MARCUS & GOSLINER (1984), JENSEN (1997)
***P. inconspicua* Bergh, 1897**	Type Locality: Sergipe (Brazil) Other localities: North Carolina, Florida, Belize, Honduras, Venezuela, Virgin Islands, Martinique, St. Vicent & the Grenadines, Grenada, Surinam, Florida, Colombia, Argentina, Tropical West Africa (Ivory Coast to Nigeria), Israel. 0–150 m.	32-40 X 55-68.0.55-68 34 X 72.0.72 30 X 64.0.64 35 X 55.0.55	up to 60	present	present	BERGH (1897), VAYSSIERE (1901), ER. MARCUS (1957, 1961), NIJSSEN-MEYER, 1965), ER. MARCUS (1957), EV. MARCUS & ER. MARCUS (1966, 1967b), MARCUS & GOSLINER (1984), MUNIAIN (1997), ARDILA & RACHELLO (2004), VALDES et al. (2006), present study
P. japonica Thiele, 1925	Type Locality: ? Kôbe (Japan). Other localities: South Korea. 0–400 m.	50-80.0.50-80	12–100	No data	No data	TSUBOKAWA et al. (1992)
P. californica MacFarland, 1966	Type Locality: Golden Gate and southeast of the Farallon Light. Other localities: California. 10–470 m.	52 X 130-145.1.130-145	up to 335	present	No data	MACFARLAND (1966), MARCUS & GOSLINER (1984), WILLAN (1987)
P. augusta Marcus & Gosliner, 1984	Type Locality: West Africa (17°2´S, 11° 40´E). 54 m.	40 X 70.0.70	32	present	present	MARCUS & GOSLINER (1984)
P. vayssierei Marcus & Gosliner, 1984	Type Locality: ? Algiers (Western Mediterranean)	35 X 65.0.65	32	No data	present	MARCUS & GOSLINER (1984)
P. bubala Marcus & Gosliner, 1984	Type Locality: Buffels Bay at Cape Point (South Africa). 10 m.	35 X 100.0.100	70	present	No data	MARCUS & GOSLINER (1984)
P. notmec Marcus & Gosliner, 1984	Type Locality: ? Israel. Other localities: Eastern Mediterranean, off Turkey. 11–140 m.	50 X 80.0.80	12–40	No data	present	MARCUS & GOSLINER (1984)
P. catherinae Dayrat, 2000	Type Locality: Coral Sea. Tropical Indo-Pacific Other localities: Indonesia, Philippines, Vanuato and the Marquesas. 352–760 m.	90 X 45.0.45	52	No data	present	DAYRAT (2000)

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Exploring Cerebral Features in Acochlidia (Gastropoda: Opisthobranchia)*

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Abstract. Histological semithin sections of the marine acochlidian species *Hedylopsis spiculifera* (Kowalevsky, 1901), *H. ballantinei* Sommerfeldt & Schrödl, 2005, *Microhedyle remanei* (Marcus, 1953) and *Asperspina murmanica* (Kudinskaya & Minichev, 1978) and of the limnic *Tantulum elegans* Rankin, 1979 were (re)examined for different cerebral features: 1) the number of cerebro-rhinophoral connectives, 2) the presence of Hancock's organs, 3) the relative position and size of the eyes, the length and diameter of the optic nerve, and the presence of an optic ganglion, and 4) cellular aggregates attached to the cerebral ganglia. We describe novel structures such as double cerebro-rhinophoral connectives in *T. elegans*, and "lateral bodies" in *H. spiculifera*, *H. ballantinei* and *A. murmanica*. Cerebral features are discussed as a promising additional set of characters for phylogenetic analysis. However, (ultra)structural comparisons of acochlidians with basal opisthobranchs and pulmonates are overdue.

Keywords. Cerebral nerves, "lateral bodies", dorsal bodies, Hancock's organ, optic ganglion.

1. INTRODUCTION

Acochlidian opistobranch gastropods show high morphological and biological diversity. However, the number of useful characters for phylogenetic analyses is still limited by the paucity of comparative data available. The central nervous system (cns) of several euthyneurous taxa was described (e.g. HASZPRUNAR & HUBER 1990; HUBER 1993; MIKKELSEN 2002), comprising data about cerebral nerves and sensory organs. The value of these data in phylogenetic studies is evident (DAYRAT & TILLIER 2002; MIKKELSEN 1996). In contrast, several of the species (re)descriptions in Acochlidia do not include any information on the cns (e.g. HAYNES & KENCHINGTON 1991; HUGHES 1991; KIRSTEUER 1973; MARCUS & MARCUS 1955, 1959; SALVINI-PLAWEN 1973; WAWRA 1979, 1980, 1988). Other authors limited their descriptions of the cns to the main ganglia on the (pre)pharyngeal nerve ring and the visceral nerve cord (e.g. BERGH 1895; BÜCKING 1933; CHALLIS 1968, 1970; DOE 1974; HERTLING 1930; KOWALEVSKY 1901; KUDINSKAYA & MINICHEV 1978; KÜTHE 1935; MARCUS 1953; MARCUS & MARCUS 1954; MORSE 1976; SWEDMARK 1968; WAWRA 1989; WESTHEIDE & WAWRA 1974). Unfortunately, the identification of the small and hardly separated ganglia on the visceral nerve cord is problematic. Even detailed histological descriptions, such as that of *Tantulum elegans* by RANKIN (1979), can be considerably misleading and thus cannot be trusted (see NEUSSER & SCHRÖDL 2007). Furthermore, very few studies give data about cerebral nerves and sensory organs reflecting the complexity of the acochlidian cns. HUBER (1993) gave a detailed overview of the cns in marine heterobranchs and determined the number of cerebral nerves in Acochlidia to only two (the labiotentacular nerve and the proximally joint oral and rhinophoral nerve) plus the static nerve. SOMMERFELDT & SCHRÖDL (2005) confirmed these three nerves plus optic nerves for *Hedylopsis spiculifera* and *H. ballantinei*. The authors emphasized the presence of large rhinophoral ganglia, from which the joint oral and rhinophoral nerve arise, and that was overlooked in *H. spiculifera* by HUBER (1993). The terminology and the homology of the different cerebral nerves in Acochlidia are still uncertain.

Data about sensory organs are sparse, often consisting only in the affirmation of presence or absence of easily identified structures, such as eyes (e.g. CHALLIS 1970; MARCUS 1953; MARCUS & MARCUS 1955; WESTHEIDE & WAWRA1974). Hancock's organs, the primary chemosensory organs in architectibranchs and cephalaspideans (MIKKELSEN 1996, 2002), were thought to be absent in Acochlidia (e.g. NEUSSER et al. 2006; SOMMERFELDT & SCHRÖDL 2005; WAWRA 1987). However, Hancock's organs like structures were reported from *Microhedyle glan-*

Table 1 . Comparison of cerebral features in different acochlidian species. +: present, –: absent, ?: not detected.

species **feature**	*Hedylopsis spiculifera*	*Hedylopsis ballantinei*	*Asperspina murmanica*	*Tantulum elegans*	*Microhedyle remanei*
Double cerebro-rhinophoral connective	?	?	?	+	?
Hancock´s organ	?	?	?	+	?
Eyes	+ pigmented	+ pigmented	–	+ reduced unpigmented	–
Eyes externally visible	dorsal and lateral well visible	dorsal and lateral hardly visible	–	not visible	–
Eyes position	posterior to the rhinophores (in some distance)	slightly posterior to the rhinophores (at their base)	–	slightly anterolateral to the cerebral ganglion	–
Eye size in diameter	25 µm	30 µm	–	20 µm	–
Optic nerve	long, undulated	long, undulated	–	short. not undulated	–
Optic nerve diameter	6–7 µm	6–7 µm	–	3 µm	–
Optic ganglion (diameter)	–	–	–	+ (18 µm)	–
Lateral bodies	+	+	+	–	–
Cells above cerebral commissure	?	?	+	?	?

dulifera (Kowalevsky, 1901) and *Pontohedyle milaschewitchii* (Kowalevsky, 1901) by EDLINGER (1980a, b), and recently confirmed for *P. milaschewitchii* (JÖRGER et al. in press). Additionally, our re-examination of *Tantulum elegans* revealed the presence of a small Hancock's organ in this species too (NEUSSER & SCHRÖDL 2007).

Among representatives of four traditional acochlidian families (Hedylopsidae, Asperspinidae, Tantulidae and Microhedylidae), the present study (re)investigates a number of special cerebral nervous features using histological sections. As far as information is available, these characters are compared with other acochlidian species and are evaluated as a possible set of characters for future phylogenetic analysis.

2. MATERIAL

Serial semi-thin sections of five different acochlidian species were available for re-examination by light microscopy: one series (section thickness: 1.5 µm) of *Hedylopsis spiculifera*, Zoologische Staatssammlung München, ZSM N° 20070391 (Secche della Meloria, Livorno, Italy, September 2005) and one paratype series (section thickness: 2 µm) of *Hedylopsis suecica* Odhner, 1937, Swedish Museum of Natural History, SMNH N° 27211; *H. suecica* was considered as a synonym of *H. spiculifera* by WAWRA (1989) and confirmed by SOMMERFELDT & SCHRÖDL (2005). Five paratype series (section thickness: 2 µm) of *Hedylopsis ballantinei*, ZSM N° 20004766/1, 20004767, 20004768, 20004769 and N° 26X (Dahab, Gulf of Aqaba, northern Red Sea, October 1999). Six series (section thickness: 1.5 µm) of *Microhedyle remanei*, ZSM N° 20070079, 20070080, 20070081, 20070082, 20070083 and 20070084 (southwest of Castle Roads, Bermuda Islands, July 1999). Four series (section thickness: 1.5 µm) of *Asperspina murmanica*, ZSM N° 20062163, 20062164, 20062165 and 20062167 (Yarnyshnaya Bay, Barents Sea, Russia, August 2005). Four original paratype series (section thickness: 3 µm) and two recently prepared paratype series (section thickness: 1.5 µm) of *Tantulum elegans*, Royal Ontario Museum, Canada, ROM N° 8E1 and 2F0 (Golden Grove, St. Vincent, West Indies, July 1972). All sections, except the original paratype series of *T. elegans*, were stained with methylene blue-azure II according to RICHARDSON et al. (1960).

3. CEREBRAL FEATURES EXAMINED

3.1. Rhinophoral ganglia and cerebro-rhinophoral connectives

A comparative overview of all examined features in the different species is given in Table 1.

All species re-examined herein, except *Microhedyle remanei*, have a pair of true rhinophoral ganglia, i.e. large ganglia separated into a nuclei-free medulla and a cortex composed of cell bodies. The rhinophoral ganglia of *M. remanei* are not subdivided into cortex and medulla; instead the nuclei are distributed homogeneously all over the ganglion (see Neusser et al. 2006, fig. 3d). Serial sections of *Hedylopsis spiculifera*, *H. ballantinei* and *M. remanei* show only a single nerve (approx. 5–10 µm in diameter) that connects the cerebral ganglion to the rhinophoral one. In one specimen of *Tantulum elegans* examined, we found two nerves connecting the cerebral ganglion with the rhinophoral ganglion (Fig. 1). Both nerves are thin (approx. 7 µm in diameter) and lie close together (distance between them approx. 3µm). Nevertheless, the transition between the cerebral ganglion and the rhinophoral ganglion is well identifiable due to the presence of dark stained fibres (Fig. 1A, D).

3.2. Sensory organs

3.2.1. Hancock's organ and nerve

Paired, small and ciliated invaginations posterior to the head appendages and innervated by cerebral nerves are present in *Tantulum elegans* (see Neusser & Schrödl 2007, fig. 4b). Neither such organs of similar shape could be detected in *Hedylopsis spiculifera*, *H. ballantinei* and *Microhedyle remanei*, or cerebral nerves innervating the region where Hancock's organs are present in other acochlidian species.

3.2.2. Eyes, optic nerves and optic ganglia

Asperspina murmanica and *Microhedyle remanei* are eyeless and lack any optic nerve or optic ganglion. Both *Hedylopsis* species have pigmented lens eyes (Fig. 3A, B) that, however, differ in size and relative position. The eyes of *H. spiculifera* are clearly visible externally (Fig. 2A, B) from dorsal and lateral and reach up to 25 µm in diameter (Fig. 3A). They are located on the rather lateral side of the head (Fig. 2B), and are in some distance posterior to the rhinophores (Fig. 2A, B) and anterior of the cerebral ganglia. In contrast, the eyes of *H. ballantinei* are hardly detectable by external view (Fig. 2C) even though they are slightly larger (approx. 30 µm in diameter) (Fig. 3B). Furthermore, they are situated closer together and are just posterior to the rhinophores (Fig. 2C). The optic nerves show approx. 6-7 µm in diameter in both species (Fig. 3A, B). They arise from the rhinophoral ganglia and are highly undulated. An optic ganglion is absent in *H. spiculifera* as well as in *H. ballantinei*. In contrast, *Tantulum elegans* develops a very short and thin optic nerve (approx. 3 µm in diameter) leading to a reduced unpigmented eye of approx. 20 µm in diameter (Figs. 1, 3C). The optic nerve arises from a small optic ganglion (approx. 18 µm in diameter) that is subdivided into the outer cortex and the inner medulla (Fig. 3D). It is attached laterally to the cerebral ganglion, both of which are surrounded by a thin layer of connective tissue (Fig. 3D). No nerves can be detected by light microscope examination connecting the cerebral with the optic ganglion.

3.3. Aggregates attached to the cerebral ganglia

3.3.1. "Lateral bodies"

A "lateral body" as defined herein consists of a more or less hemispherical cluster of cells that is lying laterally on the surface of each cerebral ganglion. Under a light microscope, the cells of the "lateral bodies" cannot be distinguished from the neuron bodies situated in the cortex of the cerebral ganglion. Each "lateral body" is surrounded by a separate, relatively thin sheath of connective tissue and together with the cerebral ganglion by a second common and thick one. "Lateral bodies" are present in *Hedylopsis spiculifera* (Fig. 4A), *H. ballantinei* (Fig. 4B) and *Asperspina murmanica* (Fig. 4C). The "lateral body" lacks any subdivision. The nuclei are more or less uniformly distributed over the entire "lateral body". There are no nerves visible under the light microscope connecting the cerebral ganglion with the "lateral body", and there are no nerves arising from the latter. None of the specimens examined of *Microhedyle remanei* and *Tantulum elegans* had "lateral bodies".

3.3.2. Cells near the cerebral commissure

Additionally, we could find several cells of uncertain origin and function dispersed in the connective tissue above the cerebral commissure in *Asperspina murmanica* (Fig. 4D). In contrast to the "lateral bodies", these cells are not tightly attached to each other, and are not enclosed by an individual sheath of connective tissue. No data about the presence or absence of these cells can be given for *Hedylopsis spiculifera*, *H. ballantinei* and *Tantulum elegans*, due to very compressed tissue layers.

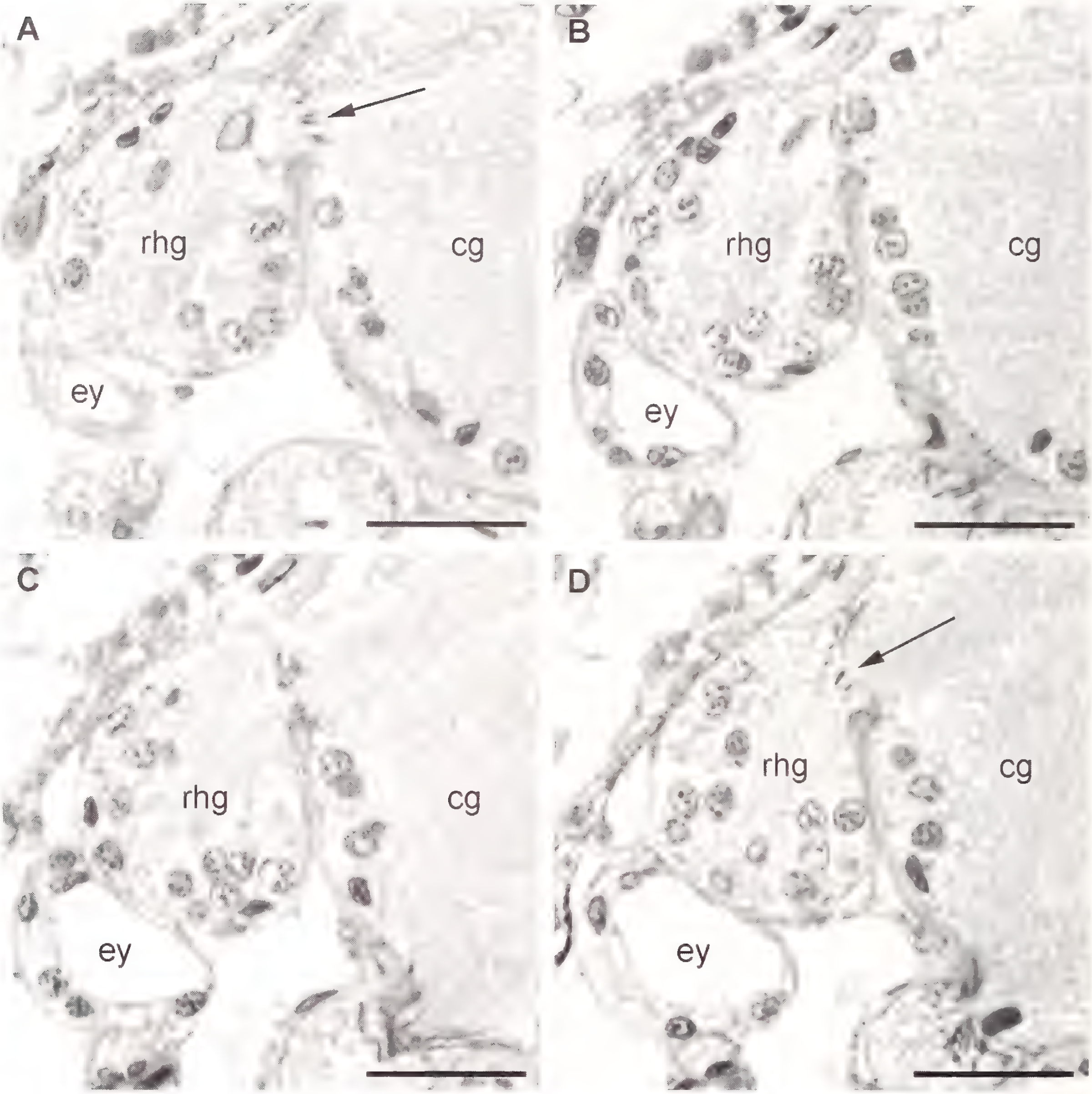

Fig. 1. Double cerebro-rhinophoral connective in *Tantulum elegans*. Four consecutive cross sections of series ROM N° 8E1, 3.slide, 6. ribbon, section N° 17–20. A: section N° 17, first cerebro-rhinophoral connective. B and C: section N° 18 and 19, respectively, without connective. D: section N° 20, second cerebro-rhinophoral connective. cg cerebral ganglion; ey eye; rhg rhinophoral ganglion; arrow, indicates fibres of the cerebro-rhinophoral connective. Scale bars A–D: 15 µm.

4. DISCUSSION

4.1. Rhinophoral ganglia and number of cerebro-rhinophoral connectives

The presence of rhinophoral ganglia were reported for *Hedylopsis spiculifera* and *Tantulum elegans* (see RANKIN 1979; WAWRA 1989), but both descriptions lack histological data of the rhinophoral ganglia. Recently, rhinophoral ganglia were described in detail for *Hedylopsis ballantinei* (see SOMMERFELDT & SCHRÖDL 2005), *Microhedyle remanei* (see NEUSSER et al. 2006), *T. elegans* (see NEUSSER & SCHRÖDL 2007) and *Pontohedyle milaschewitchii* (see JÖRGER et al. in press). Due to their position anterodorsally of the cerebral ganglia and their similar innervation the homology of the rhinophoral ganglia can be assumed for all acochlidian species studied herein. In contrast to *Hedylopsis* species, *Asperspina murmanica* and *T. elegans*, rhinophoral ganglia of *P. milaschewitchii* and *M. remanei* are not separated into medulla and cortex. The presence

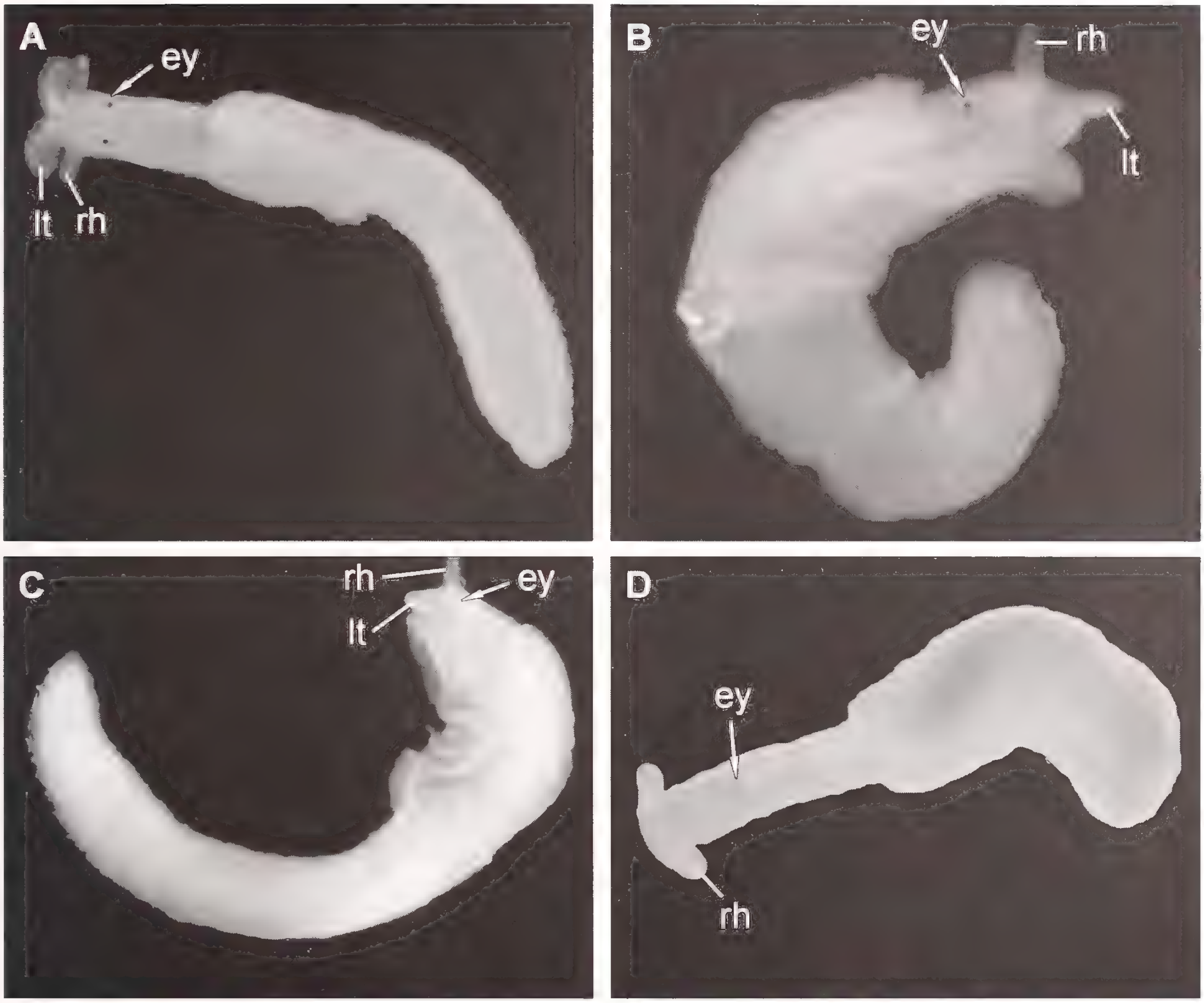

Fig. 2. Position of eyes in different acochlidian species, external view. A: *Hedylopsis spiculifera*, dorsal view, length 3.5 mm. B: *Hedylopsis spiculifera*, lateral view, length 3.5 mm. C: *Hedylopsis ballantinei*, lateral view, length 5 mm. D: *Pontohedyle milaschewitchii*, dorsal view, length 2.5 mm. ey eye; lt labial tentacle; rh rhinophore.

of rhinophoral ganglia within *P. milaschewitchii* that is lacking any rhinophores might be explained by a modified, e.g. neurosecretory function. *Microhedyle remanei*, however, possesses rhinophores and cell bodies evenly distributed within the rhinophoral ganglia.

Of all the specimens here studied, the double connection between the cerebral ganglia and rhinophoral ganglia could only be detected in one specimen of *Tantulum elegans*, and is only clearly visible on the right side of the nervous system. Unfortunately, the identification of these thin nerves depends critically upon preservation and staining conditions as well as on the cutting plane. Tiny nerves can thus be overlooked and easily misinterpreted, or be invisible even on semi-thin serial sections. While "detected" usually means "present", "not detected" does not necessarily mean "absent". The cerebro-rhinophoral connective has been identified by the presence of dark stained fibres. HASZPRUNAR (1985, figs. 19, 20) described similar fibres occurring at the transition between two different ganglia in *Discotectonica discus* Philippi, 1844. A double cerebro-rhinophoral connective has also been found in *Pontohedyle milaschewitchii* (see JÖRGER et al. in press); both nerves are even thinner than those in *T. elegans*. There is no reliable data on further acochlidians.

HASZPRUNAR & HUBER (1990) described a double cerebro-rhinophoral connective for the enigmatic opisthobranchs *Rhodope veranii* Kölliker, 1847 and *Rhodope transtrosa* Salvini-Plawen, 1989, as well as a double connective attaching the cerebral ganglion with the procerebrum in the pulmonate *Smeagol manneringi* Climo, 1980. In fact, the double cerebro-rhinophoral connective of the acochlidian cns resembles the general pulmonate condi-

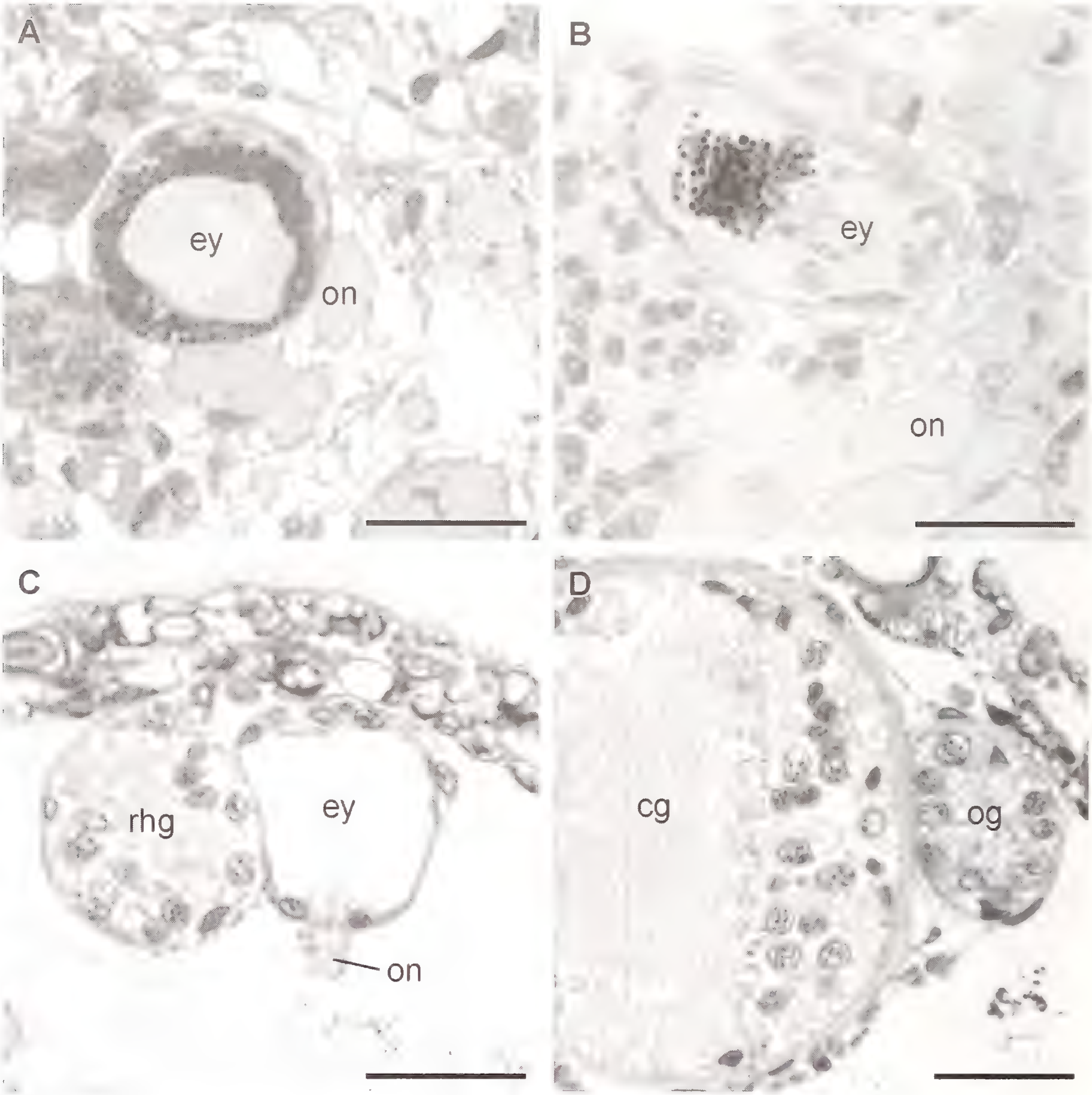

Fig. 3. Eyes and optic ganglion (cross sections). A: Pigmented eye in *Hedylopsis spiculifera* ZSM N° 20070391. B: Pigmented eye in *Hedylopsis ballantinei* ZSM N° 20004766/1. C: Unpigmented eye in *Tantulum elegans* ROM N° 8E1. D: Optic ganglion attached to the cerebral ganglion in *Tantulum elegans* ROM N° 8E1. cg cerebral ganglion; ey eye; og optic ganglion; on optic nerve; rhg rhinophoral ganglion. Scale bars A–D: 15 µm.

tion (VAN MOL 1967). Therefore, the potential homology of acochlidian rhinophoral ganglia to the procerebrum of pulmonates should be investigated in detail.

4.2. Sensory organs

4.2.1. Hancock's organ

We were not able to detect any Hancock's organ like structures in the species examined herein except for *Tantulum elegans* which shows a pair of epidermal folds on the side of the head (NEUSSER & SCHRÖDL 2007). Such folds were reported for *Pontohedyle milaschewitchii* and *Microhedyle glandulifera* and regarded as Hancock's organs by EDLINGER (1980a, b), i.e. as true homologues of the primary chemosensory organs in architectibranchs and cephalaspids (see MIKKELSEN 1996). According to their similar position, cerebral innervation, (although more tiny) structure, and probable sensory function, a general homology can be suspected. Some doubts persist, such as the

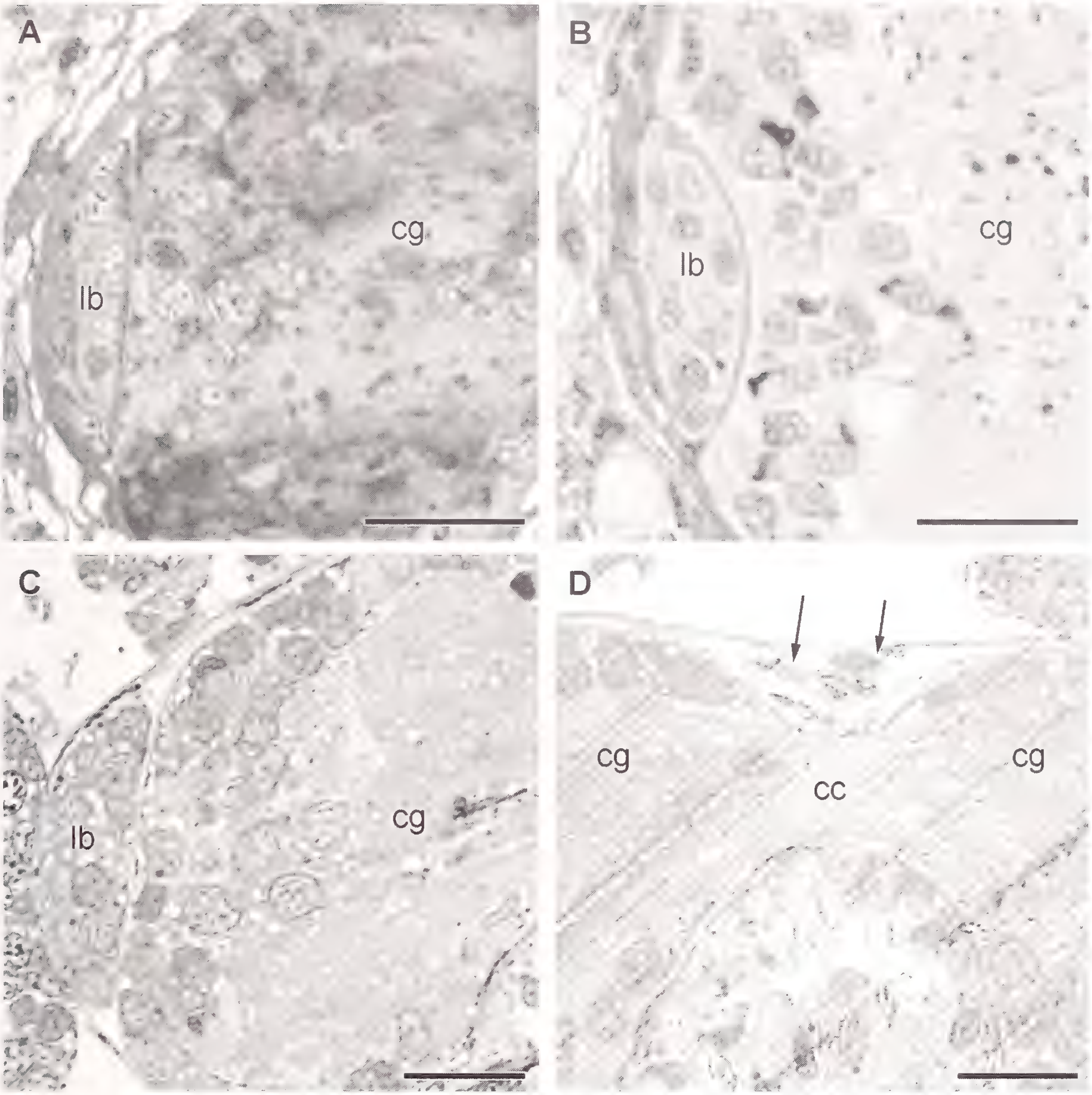

Fig. 4. Aggregates attached to the cerebral ganglia (cross sections). A: "Lateral body" in *Hedylopsis spiculifera* ZSM N° 20070391. B: "Lateral body" in *Hedylopsis ballantinei* ZSM N° 20004766/1. C: "Lateral body" in *Asperspina murmanica* ZSM N° 20062163. D: Cells above cerebral commissure in *Asperspina murmanica* ZSM N° 20062163. cc cerebral commissure; cg cerebral ganglion; lb "lateral body"; arrow, cells near cerebral commissure. Scale bars A–D: 15 µm.

yet unclear homology of euthyneuran cerebral nerves, the unknown origin of the Acochlidia and reports of acochlidian "Hancock's organs" from only a few and supposedly derived microhedylid species, i.e. *P. milaschewitchii* and *M. glandulifera,* and the enigmatic *T. elegans.*

4.2.2. Eyes, optic nerves and optic ganglia

In the past, the description of acochlidian eyes often was limited to the affirmation of presence or absence of these sensory organs. Eyes are absent in all *Asperspina* species, *Microhedyle remanei*, *Ganitus evelinae* Marcus, 1953, *Paraganitus ellynnae* Challis, 1968 and *Pontohedyle verrucosa* Challis, 1970 (see Challis 1968, 1970; Kudinskaya & Minichev 1978; Marcus 1953; Morse 1976; Salvini-Plawen 1973; Swedmark 1968). Our results show that the position, size and development of eyes in Acochlidia examined herein differ considerably.

The eyes of *Hedylopsis spiculifera* are clearly visible externally from a dorsal and lateral view. In the freshwater acochlidian species *Strubellia paradoxa* (Strubell, 1892) and *Acochlidium fijiense* Haynes & Kenchington, 1991 the eyes are clearly observable only in lateral view (unpubl. data of MS). In contrast, the eyes of the marine *Microhedyle glandulifera* (see Kowalevsky 1901; Marcus & Marcus 1955; Odhner 1952), *Hedylopsis ballantinei* (Fig. 2C) and *Pontohedyle milaschewitchii* (Fig. 2D) are externally not that clearly visible through the head tissue. Westheide & Wawra (1974) observed that eyes of *Parhedyle cryptophthalma* (Westheide & Wawra, 1974) were not visible externally in living specimens, and only as two small pigmented spots in preserved specimens. Eyes in *Pseudunela cornuta* (Challis, 1970) are poorly developed and not visible externally (Challis 1970, as *Hedylopsis cornuta*).

The eyes of *Hedylopsis spiculifera* and *H. ballantinei* are both located dorsolaterally in the body cavity; while the eyes of *H. ballantinei* are situated at the base of the rhinophores, in *H. spiculifera* they are somewhat more posteriorly. A similar dorsolateral eye position at or close to the base of the rhinophores is already known from the limnic acochlidian species *Acochlidium amboinense* Strubell, 1892, *Palliohedyle weberi* (Bergh, 1895) and *Strubellia paradoxa* (see Bergh 1895; Bücking 1933; Küthe 1935). In contrast, the eyes of *Pontohedyle milaschewitchii* are located more posteriorly and closer together (Fig. 2D). Westheide & Wawra (1974) described a similar eye position in the marine acochlidian *Parhedyle cryptophthalma*.

The optic nerve is short in *Strubellia paradoxa* (see Küthe 1935). The well-developed eyes of *Acochlidium amboinense*, *Palliohedyle weberi* and *S. paradoxa* were described as attached anterodorsally to anterolaterally on the cerebral ganglia (Bergh 1895; Bücking 1933; Küthe 1935), thus the optic nerves are probably short as well. The eyes of *Pontohedyle milaschewitchii* are directly attached to the cerebral ganglia (Jörger et al. in press), as are the eyes of *Parhedyle cryptophthalma*, *Microhedyle nahantensis* (Doe, 1974), *M. glandulifera* and *M. odhneri* (Marcus, 1955) (see Doe 1974; Marcus & Marcus 1955; Westheide & Wawra 1974). The optic nerve is moderately long but thin in *Tantulum elegans*, while long and thick in both *Hedylopsis* species. The long optic nerves observed herein may be phylogenetically informative in Acochlidia.

All eyes described for Acochlidia are pigmented, except those of *Tantulum elegans* (present study) and of *Microhedyle nahantensis* (see Doe 1974). The "poorly developed" eyes of *Pseudunela cornuta* described by Challis (1970) should be reinvestigated.

The eye size differs within the species: whereas eyes of *Hedylopsis spiculifera* and *H. ballantinei* measure approx. 25 and 30 µm, respectively, eyes in *Pontohedyle milaschewitchii* reach approx. 20 µm (Jörger et al. in press). The largest eye size known from an acochlidian species is 0.52 mm and was reported for the limnic *Palliohedyle weberi* (see Bergh 1895).

The optic ganglion in *Tantulum elegans* was first described by Neusser & Schrödl (2007) and is regarded to be a true ganglion with subdivision into cortex and medulla (see Neusser et al. 2006). More specifically, it is enclosed in a thin layer of connective tissue together with and attached to the cerebral ganglion. This feature should not be confused with the "lateral bodies" described in the present study, since the latter are lying inside the thick layer of connective tissue from the cerebral ganglion (see below). So far there are only two reports of ganglia being surrounded by a common layer of connective tissue with the cerebral ganglia: the rhinophoral ganglia of *T. elegans* (see Neusser & Schrödl 2007), and the rhinophoral ganglia of *Pontohedyle milaschewitchii* (Jörger et al. in press).

The presence of an optic ganglion only in *T. elegans* is surprising, since eyes are unpigmented in this species, while for species possessing more well-developed eyes (e.g. both *Hedylopsis* species and *Pontohedyle milaschewitchii*) this character is lacking. Either there are some unknown sensory abilities involved in at least one ontogenetic stage, or both eyes and optic ganglia are evolutionary remnants of organs in the process of being reduced. The optic ganglia of *Tantulum* do no more fuse with the rhinophoral ganglia, as may be the case in both *Hedylopsis* species with large rhinophoral ganglia bearing optic nerves. We urgently need ontogenetic evidence for the development of acochlidian central nervous structures.

The presence of optic ganglia, the origin and length of optic nerves, eye position in terms of situation and proximity to the cerebral ganglion, as well as eye size and structure should be reinvestigated in all acochlidian species, since these may be easily accessible and phylogenetically informative characters (see Mikkelsen 1996).

4.3. Aggregates attached to the cerebral ganglia

4.3.1. "Lateral bodies"

Sommerfeldt & Schrödl (2005) described "dorsal bodies" attached to the cerebral ganglion in the acochlidian *Hedylopsis ballantinei*. We herein confirm the presence of such organs for both *Hedylopsis* species and *A. murmanica*. Their position is, however, more lateral than dorsal. We thus propose to use the term "lateral bodies" for such acochlidian structures until more detailed and comparative data are available to assess their homology to pulmonate dorsal bodies.

The "lateral bodies" of the re-examined acochlidian species are characterized by a group of neuronal cells that are enclosed within the thick connective tissue layer surrounding the cerebral ganglion. The dorsal bodies of basommatophoran pulmonates consist of a pair of similar neuronal cell clusters that are, however, enclosed in a thin sheath of connective tissue, and are situated dorsally on the cerebral ganglia. Basommatophoran dorsal bodies can lie close together and appear as one group in *Helisoma* Swainson, 1840 and *Planorbarius* Duméril, 1806, or they can be distinguished as two separate tissue masses, as in *Ancylus* Mueller, 1774, *Lymnaea* Lamarck, 1801 and *Siphonaria* Sowerby, 1823 (SALEUDDIN 1999; SALEUDDIN et al. 1997; TAKEDA & OHTAKE 1994).

SOMMERFELDT & SCHRÖDL (2005) described the "lateral bodies" of *Hedylopsis spiculifera* and *H. ballantinei* being subdivided into an outer cortex and an inner medulla. According to SALEUDDIN (1999), most of the dorsal bodies of basommatophoran pulmonates develop a cortex with nuclei and an inner medulla with cell processes that lie very close to the cerebral ganglia. In "lateral bodies" of *H. spiculifera*, *H. ballantinei* and *Asperspina murmanica*, no such clear subdivision into cortex and medulla was found; instead all nuclei are distributed more or less uniformly. Similarly, the basommatophoran pulmonate *Siphonaria pectinata* Linnaeus, 1758 is described to possess dorsal bodies without clear separation into cortex and medulla (SALEUDDIN et al. 1997).

The function of the "lateral bodies" in *Hedylopsis spiculifera*, *H. ballantinei* and *Asperspina murmanica* is unclear. Due to the absence of visible nerves arising from these aggregations, the "lateral bodies" are possibly not sensory but secretory organs. The role of dorsal bodies in pulmonates as an endocrine organ involved in female reproduction is quite well known (SALEUDDIN 1999). Furthermore a putative endocrine gland, called the juxtaganglionar organ, has been described in several opisthobranch species (e.g. SWITZER-DUNLAP 1987). However, the homology of these structures is still unclear. Future studies by means of transmission electron microscopy and (immuno)histochemical studies are needed to understand homologies and functions. Disregarding our deficient knowledge, within acochlidians the presence of "lateral bodies" in members of Hedylopsidae, Asperspinidae and Tantulidae versus their absence in two members of Microhedylidae (*Pontohedyle milaschewitchii, Microhedyle remanei)* may represent characters with a phylogenetic signal.

4.3.2. Cells near the cerebral commissure

For the first time in an acochlidian species we describe several cells that are loosely dispersed within the connective tissue above the cerebral commissure in *Asperspina murmanica*. Due to its position such a cell aggregation resembles the dorsal bodies of stylommatophoran pulmonates (e.g. *Theba pisana* Mueller, 1774, *Helix aspersa* Mueller, 1774 and *Achatina fulica* Ferussac, 1821) which were described as diffusely scattered cells within the connective tissue sheath of the cerebral ganglion and located near the cerebral commissure (SALEUDDIN 1999; SALEUDDIN et al. 1997; TAKEDA & OHTAKE 1994). The presence, structure, origin and function of these cells in acochlidians cannot be revealed by light microscopy alone but requires ultrastructural studies.

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The cephalic sensory organs of *Acteon tornatilis* (Linnaeus, 1758) (Gastropoda Opisthobranchia) – cellular innervation patterns as a tool for homologisation*

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Abstract. Gastropoda are guided by several sensory organs in the head region, referred to as cephalic sensory organs (CSOs). This study investigates the CSO structure in the opisthobranch, *Acteon tornatilis* whereby the innervation patterns of these organs are described using macroscopic preparations and axonal tracing techniques.

A bipartite cephalic shield and a lateral groove along the ventral side of the cephalic shield was found in *A. tornatilis*. Four cerebral nerves can be described innervating different CSOs: N1: lip, N2: anterior cephalic shield and lateral groove, N3 and Nclc: posterior cephalic shield. Cellular innervation patterns of the cerebral nerves show characteristic and constant cell clusters in the CNS for each nerve.

We compare these innervation patterns of *A. tornatilis* with those described earlier for *Haminoea hydatis* (STAUBACH et al. *in press*). Previously established homologisation criteria are used in order to homologise cerebral nerves as well as the organs innervated by these nerves. Evolutionary implications of this homologisation are discussed.

Keywords. *Haminoea hydatis,* Cephalaspidea, axonal tracing, homology, innervation patterns, lip organ, Hancock´s organ.

1. INTRODUCTION

Gastropoda are guided by several organs in the head region which are assumed to have primarily chemo- and mechanosensory functions (AUDESIRK 1979; DAVIS & MATERA 1982; BICKER et al.1982; EMERY 1992; CHASE 2000; CROLL et al. 2003). In Opisthobranchia, these cephalic sensory organs (CSOs) present an assortment of forms including rhinophores, labial tentacles, oral veils, Hancock´s organs and cephalic shields. Recent investigations of CSOs in Opisthobranchia have focussed primarily on functional aspects (CROLL 1983; BOUDKO et al. 1999; CROLL et al. 2003) while homology of the different types of CSOs in different taxa has never been investigated in detail. We want to clarify their homology in separate evolutionary lineages so as to elucidate key questions regarding character evolution and phylogeny.

Acteon tornatilis belongs to the subgroup Acteonoidea, formerly ascribed to the basal Cephalaspidea (ODHNER 1939, BURN & THOMPSON 1998). However, recent investigations have either excluded the Acteonoidea from the Opisthobranchia (MIKKELSEN 1996) or proposed a sister group relationship of Acteonoidea and the highly derived Nudipleura (VONNEMANN et al. 2005) thus, rendering the phylogenetic position of Acteonoidea within Opisthobranchia unsettled. Acteonoidea are characterised by the presence of a prominent cephalic shield. This structure is also present in Cephalaspidea and has been considered to be an apomorphie of the Cephalaspidea (SCHMEKEL 1985). However, the structure of the cephalic shields differs considerably in Cephalaspidea and Acteonoidea with the latter possessing two distinct hemispheres while the cephalic shield in the Cephalaspidea possesses uniform structure. Therefore, common origin of both types of cephalic shields and thus homology is questionable. Further CSOs have been described in Acteonoidea and Cephalaspidea such as lip organ and Hancock´s organ (RUDMAN 1971A; RUDMAN 1971B; RUDMAN 1972a, b; RUDMAN 1972c; EDLINGER 1980).

Since the presence of these organs in members of the genus *Acteon* has been disputed by different authors (EDLINGER 1980; SCHMEKEL 1985), absolute clarification is certainly necessary . The intention of this study is to describe the structure emphasizing the innervation of the CSOs in the acteonid *A. tornatilis*. Our descriptions focus on the cellular innervation patterns reconstructed for the cerebral nerves using axonal tracing. In an earlier study (STAUBACH et al. *in press*) these cellular innervation patterns were shown to be more adequate in homologising cerebral nerves than ganglionic origins of nerves (HUBER 1993). By comparising the innervation patterns in *A. tornatilis* to previously published data on *H. hydatis* (STAUBACH et al. *in press*), we want to survey whether the preliminary characteristic cell clusters in the central nervous system (CNS) of both taxa can be identified by homologising cerebral nerves across taxa. Based on the homologisation of the nerves innervating the CSOs we want to clarify if *A. tornatilis* has homologous structures to the CSOs of Cephalaspideans. It is our intent interest that we shed light on the phylogenetic position and evolutionary history of Acteonoidea within the Opisthobranchia for future studies.

2. MATERIALS AND METHODS

2.1. Specimens

A. tornatilis (Fig. 1A) were collected in the wild at St. Michel en Greve (Brittany, France). They were then stored alive at our lab in Frankfurt. Fourty specimens measuring a shell length between 15 and 20 mm were traced directly (5 to 15 days after collecting) and five were fixed for SEM.

2.2. Tracing studies

Animals were relaxed with an injection of 7 % magnesium chloride. The central nervous system consisting of the cerebral, pleural and pedal ganglia was removed and placed in a small Petri dish containing filtered artificial seawater (ASW; Tropic Marin, Rebie-Bielefeld; GERMANY). We then followed the procedures from CROLL & BAKER (1990) for Ni^{2+}-lysine (Ni-Lys) tracing of axons. Briefly, the nerves of the right cerebral ganglion were dissected free from the connective tissue. The nerves were cut and the distal tip was gently drawn into a glass micropipette using suction provided by an attached 2.5 ml syringe. Subsequently, the saline in the micropipette was replaced by a Ni-Lys solution (1.9g $NiCl\text{-}6H_2O$, 3,5 g L-Lysine freebase in 20 ml double distilled H_2O). The preparation was then incubated for 12–24 hours at 8° C to allow transport of the tracer. The micropipette was then removed and the ganglia were washed in ASW three times. The Ni-Lys was precipitated by the addition of five to ten drops of a saturated rubeanic acid solution in absolute Dimethylsulfoxide (DMSO). After 45 minutes the ganglia were transferred to 4 % paraformaldehyde (PFA) and fixed for 4–12 hours at 4° C. Thereafter the ganglia were dehydrated in an increasing ethanol series (70/80/90/99/99% 10 minutes each), cleared in methylsalicylate and mounted on an objective slide dorsal side up in Entellan (VWR International) and covered with a cover slip. Ten replicates were prepared for each cerebral nerve of *A. tornatilis*. Samples with only a partial staining of the nerve were not used because of possible incomplete innervation patterns. Our criterion for a well-stained preparation was a dark blue stained nerve indicating intact axons (FREDMAN 1987). The Ni-Lys tracings were analysed by light microscopy (Leica TCS 4D). Camera lucida drawings were digitalised following the method of COLEMAN (2003) adapted for CorelDRAW 11. The somata in the innervation scemes occurs in all replicates. Somata only occurring in single samples are not considered part of the schematics. The axonal pathways are estimated over all replicates. Additionally, we tested for asymmetries making axonal tracings ($n = 2$ to 3) for each cerebral nerve of the left cerebral ganglion.

2.3. Scanning electron microscopy studies

The specimens were relaxed by an injection of 7 % $MgCl_2$ in the foot. Thereafter, the entire head region was dissected from the rest of the animal. The CSOs were fixed in 2,5 % glutaraldehyde, 1 % paraformaldehyde in 0,1M phosphate buffer (pH 7,2) at room temperature. For the SEM, the fixed CSOs were dehydrated through a graded acetone series followed by critical point drying (CPD 030, BAL-TEC). Finally, they were spattered with gold (Sputter-Coater, Agar Scientific) and examined with a Hitachi S4500 SEM. All photographs were taken using DISS (Digital Image Scanning System – Point Electronic) and subsequently adjusted for brightness and contrast with Corel PHOTO-PAINT 11.

3. RESULTS

3.1. Organisation and innervation of the cephalic sensory organs

A. tornatilis possesses a prominent bipartite cephalic shield (cs) in which each hemisphere of this shield is divided into an anterior and a posterior lobe (Figs. 1A and B). Eyes are embedded deeply within the tissue of the shield. Along the lateral margin of the anterior lobe of the cephalic shield a groove is present (Fig. 1B, 2A). Hidden under the cs and above the foot, the mouth opening is situated at the median frontal edge (Fig. 2B) surrounded by the lip (not visible in Figure 2B). We found four nerves innervating the CSOs (Fig.1B). The N1 (Nervus oralis) provides innervation to the lip and small median parts of the anterior cephalic shield. The bifurcated N2 (Nervus labialis/labiotentacularis) innervates the complete anterior cephalic shield whereby the groove at the ventral anterior lobe of the cephalic shield is especially innervated. The small N3 (Nervus tentacularis/rhinophoralis) innervates a little region of the posterior cephalic shield. The Nclc (Nervus clypei capitis) innervates the largest hind part of the posterior cephalic shield. We could not detect a lip organ (Fig. 2B), which according to Edlinger (1980) should comprise two small lobes on the cephalic shield above the mouth. A Hancock´s organ described by Edlinger (1980) for *A. Tornatilis*, here a folded structure separated from the cephalic shield was likewise not found in the present study.

3.2. Tracing studies

By conducting the axonal tracing studies we were able to reconstruct cellular innervation patterns for the four cerebral nerves of *A. tornatilis*. Ten replicate tracings were performed each for the N1 N2, N3 and Nclc using only the nerves of the right cerebral ganglion. The characteristic patterns of labelled somata for all nerves are shown in Figure 3A-D, including the approximate pathways of the stained axons. The identified clusters were named with abbreviations signifying the ganglion in which they are located, the nerve filled and a number indicating the order of their description (for example, Cnlc3: Cerebral Nervus labialis cluster 3). Nerve cells are grouped in clusters on the basis of their close positioning in the ganglia and the tight fasciculation of their axons projecting into the filled nerve. Asymmetries for tracings of the left nerves could not be detected.

For the N1 (n = 10) we identified six cerebral clusters (Cnoc1-6) and one pedal cluster (Pdnoc1) in each sample (Fig. 3A). The variation between the samples was restricted to very few somata in some clusters. The cerebral clusters were distributed over the whole cerebral ganglion. The pedal cluster Pdnoc1 was located on the anterior margin of the pedal ganglion above the pedal commissure. The innervation pattern of the N2 (n=10) consists of five cerebral clusters (Cnlc1-5) and three pedal clusters (Pdnlc1-3) (Fig. 3B). The cerebral clusters show distinct spatial separations and are easy to identify. The third traced cerebral nerve (n = 10) was the N3. Six cerebral (Cnrc1-6) and three pedal clusters (Pdnrc1-3) were identified (Fig. 3C). We found an additional single cluster (*Cclnrc1*) and a single soma in the left cerebral ganglion (see arrows in Fig. 3C). The contralateral cluster was located at the base of the N2 whereas the single soma was found at the root of the cerebral commissure. We observed slight intraspecific variability between the ten samples which amounted only to very few somata in some clusters. In the Nclc, the innervation (n = 10) pattern consisted of five cerebral clusters (Cncc1-5) and a single soma at the lateral margin of the cerebral ganglion above the pedal connective (Fig. 3D). Additionally we found four pedal clusters (Pdncc1-4). The Nclc had the highest amount of pedal clusters in all investigated nerves. The number of pedal somata, however, was comparable to the number of pedal somata for the N2 innervation pattern (Fig 3B).

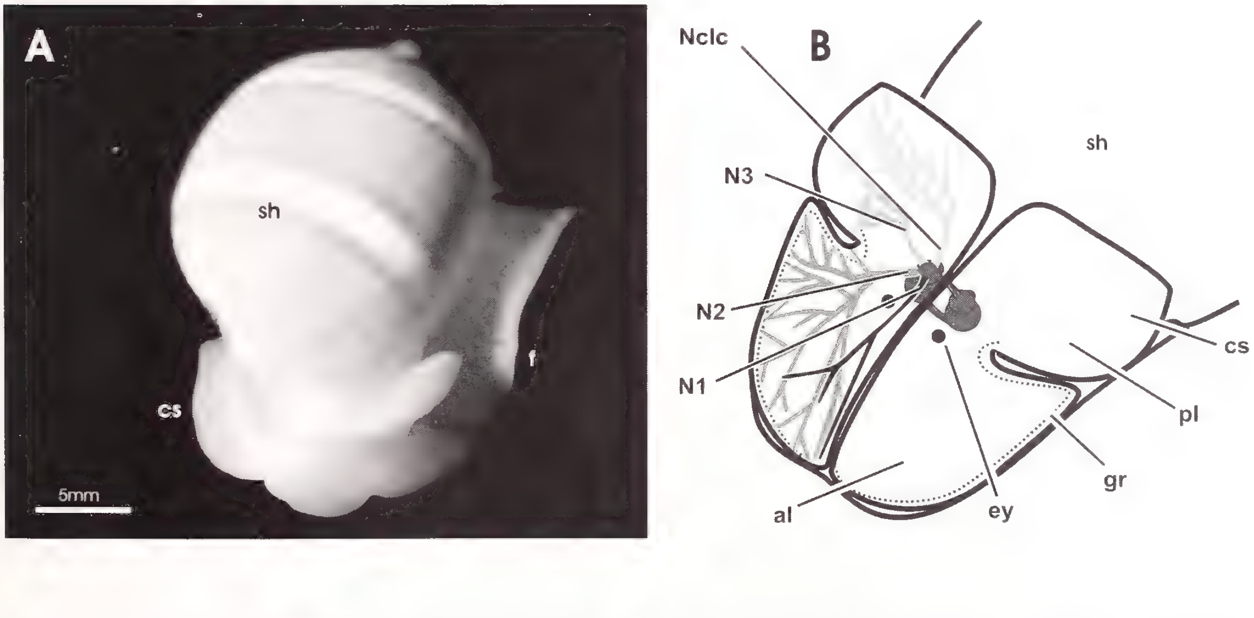


Fig. 1. **A:** Photograph of *Acteon tornatilis* with the cephalic shield visible. **B:** Schematic illustration of the CNS, the four cerebral nerves (excluding the optical nerve) and the cephalic sensory organs of *Haminoea hydatis* and *Acteon tornatilis*. Only the right cerebral nerves are shown. N1 Nervus oralis, N2 Nervus labialis, N3 Nervus rhinophoralis, Nclc Nervus clypei capitis, ey eye, gr groove, al anterior lobe, pl posterior lobe, sh shell, cs cephalic shield, f foot.

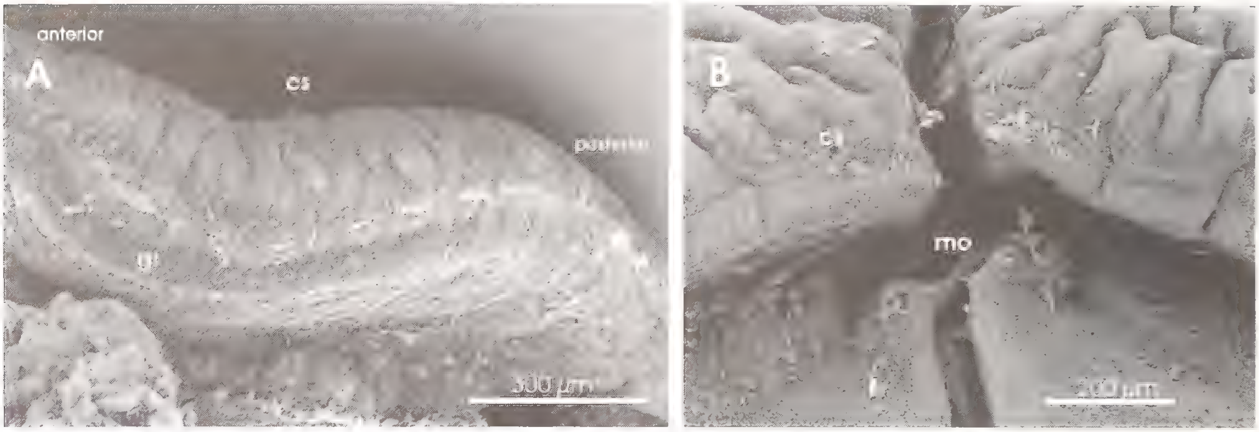


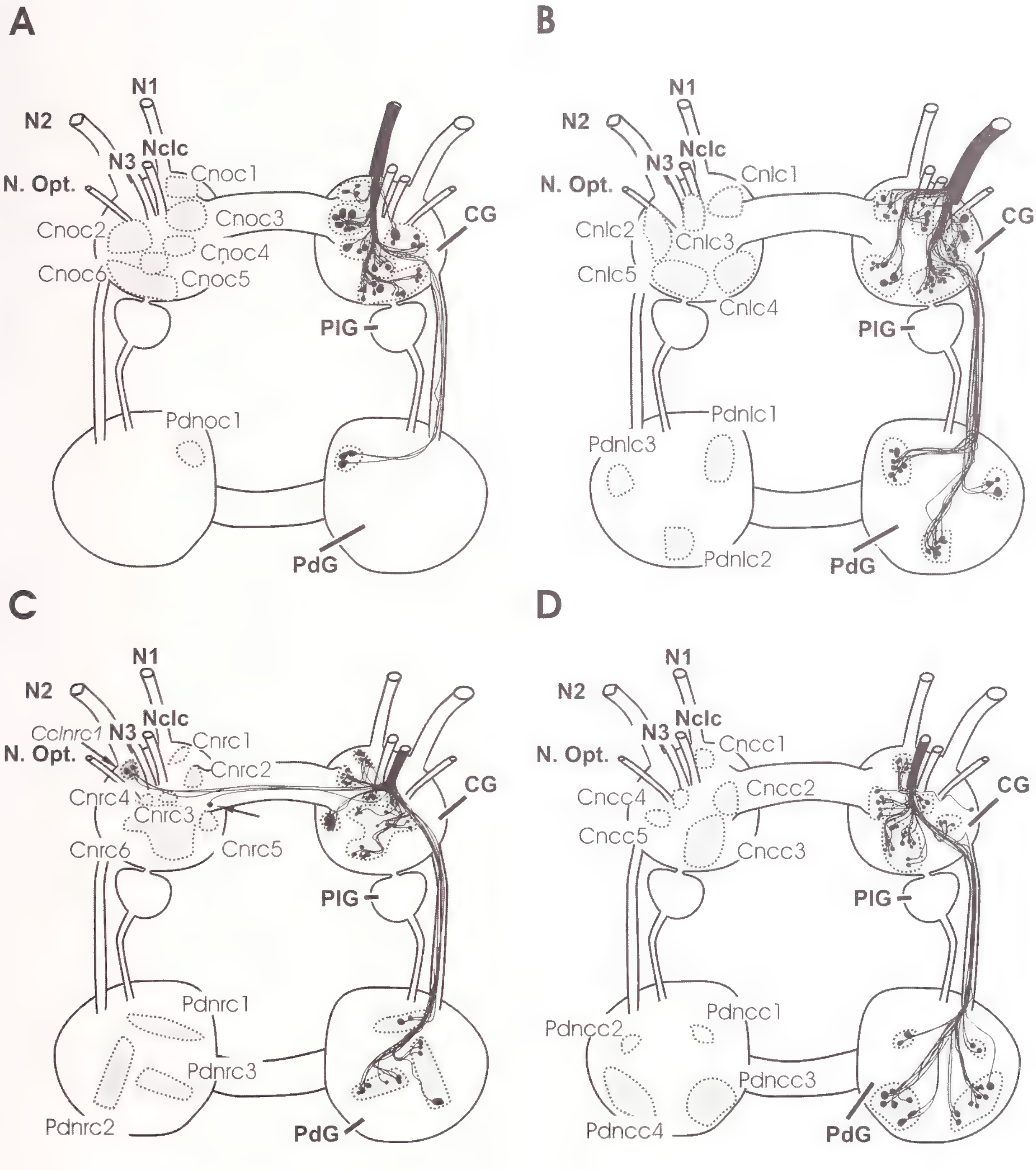
Fig. 2. A. Lateral SEM photography of the groove at the ventral surface of the cephalic shield of Acteon tornatilis. cs cephalic shield, gr groove. B. Frontal SEM photography of the mouth region of *Acteon tornatilis*. cs – cephalic shield, mo – mouth, f – foot.

4. DISCUSSION

The present study demonstrates the constancy of nervous structures in the opisthobranch mollusc. Throughout our investigation of several individuals of the acteonid, *Acteon tornatilis* we found uniform innervation patterns of the head region via four cerebral nerves, which can be attributed to characteristic neuronal cell clusters in the CNS. These cellular innervation patterns in *A. tornatilis* show an extremely high congruence with the cellular innervation patterns described for the four cerebral nerves of *Haminoea hydatis* (STAUBACH et al. in press).

In the N1, the number of cerebral clusters as well as the position of these clusters to each other is the same in *A. tornatilis* and *H. hydatis*. However, we found some differences in the size and number of somata when comparing both species. Additionally, we could not detect a pleural, a parietal and a pedal cluster in *A. tornatilis,* which were described for *H. hydatis*. This may be due to the differences in the peripheral innervation area of the N1. In *A. tornatilis* it only provides for the lip and very small parts of the median cephalic shield whereas in *H. hydatis,* it innervates the lip and large parts of the anterior cephalic shield. For the second nerve, the N2 (Nervus labialis), we nearly found no differences between the presence and distributions of the cell clusters for both species. The only ostentatious difference was the lack of a single pedal soma and its contra-lateral analogue in *A. tornatilis*. In the Nclc (Nervus clypei capitis), the difference between the two species was also reduced to the presence of a single cerebral soma in *A. tornatilis*. In contrast to the three nerves described above, we found a prominent difference in the structure of the N3 when comparing *Acteon* and *Haminoea*. On the other hand, in *H. hydatis* the N3 terminates in a rhinophoral ganglion. Such a ganglion is missing in *A. tornatilis*. Hence, we expected considerable differences in the cellular innervation patterns for the N3 of these species. However, these differences were marginal and only amounted to the lack of one single cell soma in the cerebral ganglion of *A. tornatilis*. This implies that basic innervation patterns of the N3 are probably the same in both species. Additional functions of the N3 processed in the rhinophoral ganglion can be proposed for *H. hydatis*. These functions are probably related to the Hancock´s organ, which is innervated by nerves originating in the rhinophoral ganglion (STAUBACH et al. *in press*). We were unable to locate such an organ in *A. tornatilis* in contrast to earlier descriptions (EDLINGER 1980).

Upon comparing the innervation patterns presented here for *A. tornatilis* with those for *H. hydatis* (STAUBACH et al. *in press*) we find constant features of these patterns across species. This is congruent with other findings that neuronal structures in the central nervous system of molluscs and other invertebrates seem to be highly conserved (CROLL 1987; ARBAS 1991; HAYMAN-PAUL 1991; KUTSCH & BREIDBACH 1994; NEWCOMB et al. 2006). Hence, we postulate the N1 of *A. tornatilis* to be homologous to the N1 (Nervus oralis) described by HUBER (1993) for Cephalaspideans. Additionally, we postulate homologies of the N2 and the N3 of *A. tornatilis* to the N2 (Nervus labialis) and N3 (Nervus rhinophoralis) of Chepalaspideans. This is congruent to the assumption of HOFFMANN (1939) that the c3 (after VAYSSIÈRE 1880) of *H. hydatis* represents the Nervus labialis and the c4 represents the Nervus tentacularis, here a synonym for the Nervus rhinophoralis (HUBER 1993). Our data cannot support EDLINGER'S (1980) description of independent nerves for the lip organ (N1 after Edlinger 1980) and the anterior Hancock`s organ (N2 after Edlinger 1980). The Nclc of *A. tornatilis* also seems to be homologous to the Nclc of Cephalaspideans (Huber


A
N1
N2
Nclc
N3
N. Opt.
Cnoc1
Cnoc2
Cnoc3
Cnoc4
Cnoc5
Cnoc6
CG
PlG
Pdnoc1
PdG
B
N1
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N3
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Cnlc1
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Cncc4
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PlG
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Pdncc4
PdG

Fig. 3. Schematic outline of cell clusters providing the N1 (**A**), N2 (**B**), N3 (**C**) and Nclc (**D**) of *Acteon tornatilis*. The size and position of the somata were digitalized from a camera lucida drawing, the distribution of the axons are averaged from all replicates. N1 Nervus oralis, N2 Nervus labialis, N3 Nervus rhinophoralis, Nclc Nervus clypei capitis, N. opt. Nervus opticus, CG cerebral ganglia, RhG rhinophoral ganglia, PlG pleural ganglia, PdG pedal ganglia.

1993). HOFFMANN (1939) described the same nerve as the Nervus proboscidis. We define this nerve however, as Nervus clypei capitis according to HUBER (1993).

Considering the homologisation of the cerebral nerves in light of their neurological origin, neuro-anatomics and nervous innervation patterns, we postulate hypotheses of homologies respective of the organs innervated by these nerves. Thus, we consider the lip of *A. tornatilis* to be homologous to the lip of Cephalaspideans (HUBER 1993) since both organs are innervated by the N1. The same holds true for the small median parts of the cephalic shield in *Acteon* and the anterior cephalic shield of *Haminoea*. We could not find a lip organ in *A. tornatilis* as described by EDLINGER (1980), but we detected a groove at the ventral side of the anterior cephalic shield. This groove is innervated by the N2 as is the lip organ of Cephalaspideans (HUBER 1993). Therefore, we postulate this groove to be homologous to the lip organ. This hypothesis is also supported by data on immunoreactivity against several neurotransmitters. In the groove of *A. tornatilis* as well as in the lip organ of *H. hydatis,* characteristic sub-epidermal sensory neurons containing catecholamines could be found in high density indicating that both organs are involved in contact chemoreception (S. FALLER, Frankfurt, pers. comm. 2007).

The N2 of *Haminoea* is divided into two branches which are described as two single nerves by EDLINGER (1980). The first or inner branch provides the lip organ as described earlier. The second, outer branch is related to the anterior Hancock´s organ (EDLINGER 1980; HUBER 1993). In *Acteon* we also found two branches of the N2: the inner one providing the largest part of the groove whereas the outer branch is restricted to a small region between the anterior and posterior lobe of the cephalic shield. Therefore, this latter region may be homologous to the anterior Hancock´s organ of *H. hydatis* and not to the posterior Hancock´s organ as described by EDLINGER (1980).

The N3 of *A. tornatilis* provides a large part of the posterior cephalic shield but no identifiable posterior Hancock´s organ. Additional immunohistochemical and ultrastructural investigations could also not detect a posterior Hancock´s organ in *A. tornatilis* (S. FALLER, Frankfurt, pers. comm. 2007; GÖBBELER & KLUSSMANN-KOLB *in press*). The posterior parts of the cephalic shields in *Acteon* and *Haminoea* are probably equally homologous as both where innervated by the Nclc.

The lack of a posterior Hancock´s organ in *A. tornatilis* might be due to three different reasons: 1. the ancestor of *A. tornatilis* never had a posterior Hancock´s organ; 2. the posterior cephalic shield of *A. tornatilis* may be a homologous structure to the posterior Hancock´s organ of *H. hydatis;* and 3. the posterior Hancock´s organ has secondarily been reduced in *A. tornatilis*.

The first hypothesis is rather implausible since we found a distinct N3 with conserved cellular innervation patterns in the central nervous system. If the ancestor of A. tornatilis never had a posterior Hancock´s organ, this nerve and associated neural structures should be lacking. Moreover, a Hancock´s organ has been described for other Acteonoidea (RUDMAN 1971a, b; RUDMAN 1972a, b; RUDMAN 1972c). If we consider the second explanation for lack of a posterior Hancock´s organ in *A. tornatilis,* we imply that the posterior cephalic shield in this species, innervated by the N3, presents a sensory organ as the Hancock´s organ in Cephalaspidea. However, immunohistochemical and ultrastructural investigations of the respective epithelia in *A. tornatilis* do not indicate a sensory function at all (S. FALLER, Frankfurt, pers. comm. 2007; GÖBBELER & KLUSSMANN-KOLB *in press*). We reject this hypothesis of homology of the posterior cephalic shield in *A. tornatilis* and posterior Hancock´s organ in *H. hydatis* since we found no evidence for a function of the posterior cephalic shield as an olfactory sensory organ. Moreover, the posterior cephalic shield is mostly innervated by the Nclc and not by the N3. The third hypothesis regarding the reduction of a Hancock´s organ seems to be the most plausible when the habitat and the food sources of *A. tornatilis* in comparison to *H. hydatis* are considered. The posterior Hancock´s organ is believed to be an olfactory sensory organ (AUDESIRK 1979; EMERY 1992). *H. hydatis* feeds on green algae which occur in patches in open water whereas *A. tornatilis* is a predator of soft invertebrates living up to ten centimeters in solid sand (FRETTER 1939; YONOW 1989; own investigations). In such an environment, an olfactory sensory organ is not plausible since olfaction or distance chemoreception is generally associated with water currents, which are not substantial in a sandy substrate habitat. Here, a contact chemoreceptor, which is located near the edge of the cephalic shield is more plausible. This we witnessed in *Acteon tornatilis* via its display of a potentially chemoreceptive groove along the lateral margin of the anterior cephalic shield.

This assumption of secondary reduction of the Hancock´s organ in the endobenthic *A. tornatilis* is also supported by the fact that a Hancock´s organ has been described for other epibenthic Acteonoidea (e. g. *Bullina, Micromelo, Hydatina*) (RUDMAN 1971a, b; RUDMAN 1972a, b; RUDMAN 1972a,b,c).

Despite all discussion, homology of the described Hancock´s organs to those in Cephalaspidea cannot undoubtedly be proposed at this stage, particularly since data on innervation patterns in these acteonids are lacking to date. Moreover, current phylogenetic hypotheses (GRANDE et al.

2004; VONNEMANN et al. 2005) regarding Opisthobranchia propose an independent origin of Acteonoidea and Cephalaspidea, indicating convergent development of these sensory organs in both evolutionary lineages. Further studies will have us utilizing cellular innervation patterns for CSOs in order to compare several taxa while homologising the different types of CSOs in Opisthobranchia. This procedure will enable us to glean a better understanding of the evolution of these organs.

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Editorial

Das vorliegende Doppelheft erscheint mit großer Verspätung. Eine erste Verzögerung war durch einen finanziellen Engpass verursacht worden. In der Folge ließ der Manuskripteingang so stark nach, dass wir keine Hefte füllen konnten. Dies ist auch der Grund für die unvertretbar lange Wartezeit, die für einige Autoren entstanden ist. Wir bedauern dies sehr und entschuldigen uns dafür.

Als Ausweg aus der Krise haben wir folgendes beschlossen:

(1) Wir werden mehrere Themenhefte auflegen. Als erstes wird unter der Herausgeberschaft von R. Hutterer eine Ausgabe mit lauter Art-Neubeschreibungen erscheinen. Ein zweites Themenheft wird die Verhandlungen eines Symposiums über Agamen enthalten, herausgegeben von P. Wagner. Weitere Themenhefte sind in Vorbereitung, und wir laden ausdrücklich Kolleginnen und Kollegen ein, ein solches Heft als Gastherausgeber zu betreuen.

(2) Vom jetzigen Heft an werden Abbildungen in Farbe für die Autorinnen und Autoren kostenfrei publiziert.

(3) Sämtliche in den BzB erschienene Artikel – von Band 1 an – werden nach und nach digitalisiert und online gestellt. Sie sind unter www.bzb.zfmk.de von der website des ZFMK abrufbar.

(4) Autorinnen und Autoren dürfen die PDF-Dateien ihrer Beiträge legal im Internet verfügbar machen (solange das Original-Layout nicht verändert wird).

(5) Von Band 57 an werden zum Druck angenommene Beiträge unverzüglich elektronisch veröffentlicht. Mindestens solange die Internationalen Regeln für zoologische Nomenklatur eine Publikation von wissenschaftlichen Namen und nomenklatorischen Handlungen „unter Verwendung eines Verfahrens, welches zahlreiche identische und dauerhafte Exemplare gewährleistet“ (Artikel 8.1.3.) vorschreibt, werden wir auch eine auf Papier gedruckte Version produzieren.

Wir hoffen, auf diese Weise eine höhere Zahl guter Manuskripte zu erhalten und die Bonner zoologischen Beiträge zu einem attraktiven Publikationsort zu machen.

Michael SCHMITT, Schriftleiter

The present double issue have been greatly delayed. An initial delay was caused by a financial bottleneck, which was later confounded by the submission of fewer and fewer manuscripts, and consequently we could not complete an issue. This is apparently also the reason for the dramatic setback of contributions from some authors. We deeply regret this inconvenience and apologise for it.

As a possible loophole we decided the following:

(1) We shall publish several Special Issues. First, R. Hutterer will act as guest editor for an upcoming issue containing exclusively numerous species descriptions. A second Special Issue will be devoted to the proceedings of a symposium on Agamidae, edited by P. Wagner. Additional Special Issues are in preparation, and we explicitly invite interested colleagues to publish such issues as guest editors.

(2) From this issue onwards, all colour illustrations will be published free of charge.

(3) All articles ever published in BzB will – step by step – be put online. They can be downloaded from www.bzb.zfmk.de.

(4) Authors are entitled to distribute their contributions as PDFs freely over the internet, as long as they do not alter the original layout.

(5) From Volume 57 onwards, contributions accepted for publication will immediately be published electronically. At least as long as the International Code of Zoological Nomenclature requires publication of new names and nomenclatural acts by means of "a method that assures numerous identical and durable copies" we shall continue to produce a version printed on paper.

With this anticipated increase in exposure and turn around time resulting from the above upgrades, we hope to receive a higher number of high quality manuscripts and to make the Bonner zoologische Beiträge a more attractive publication option.

Michael SCHMITT, editor-in-chief

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In memoriam Günther Osche

7.8.1926–2.2.2009

Nach einer kurzen, aber schweren Krebserkrankung starb am Montag, 2. Februar 2009, Prof.Dr.Dr.h.c. Günther Osche in Freiburg im Breisgau in seiner Wohnung im Kreis seiner Familie. Er wurde am 7. August 1926 als Sohn eines Bankangestellten in Haardt in der Nähe von Neustadt an der Weinstraße geboren. Seine Eltern zogen aber schon ein Jahr nach seiner Geburt nach Nürnberg, wo er aufwuchs. Dieser Stadt blieb er bis zu seinem Tod treu.

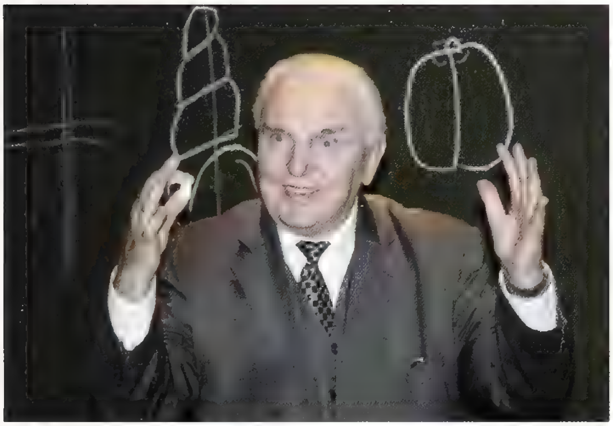

Fig. 1. Prof.Dr.Dr.h.c. Günther Osche, September 30, 2006 (Photo: M. Schmitt).

Schon als Kind und Jugendlicher war Günther Osche begeistert für die Natur, im besonderen für die Tiere, und ganz besonders für die Vögel. Mit 16 Jahren musste er Flakhelfer werden, mit siebzehn wurde er, nach einem Notabitur, zum Kriegsdienst eingezogen. Im November 1944, er war gerade einmal achtzehn Jahre alt, wurde er schwer an beiden Beinen verwundet, wovon eine lebenslange Gehbehinderung blieb.

Günther Osche studierte vom Wintersemester 1946 an Biologie an der Universität Erlangen und wurde dort mit einer unter der Betreuung von Prof.Dr. Hans-Jürgen Stammer angefertigten Dissertation über die Systematik, Phylogenie und Ökologie der Gattung *Rhabditis* (Nematoda) am 10. Juni 1951 promoviert. Im selben Jahr heirateten er und Elisabeth Riedel.

Nach Assistenten- und Dozentenzeit in Erlangen wurde er 1967 auf einen Lehrstuhl für Zoologie an die Universität Freiburg im Breisgau berufen. Bis zu seinem vorzeitigen Rückzug in den Ruhestand 1988 las er dort 22 mal die umfang- und gehaltreiche Vorlesung über spezielle Zoologie der Wirbellosen.

Aus der Reihe seiner 84 wissenschaftlichen Publikationen ragen besonders heraus seine Habilitationsschrift über die systematische Stellung und Phylogenie der Pentastomida (1963) und der Handbuchbeitrag über die „Grundzüge der allgemeinen Phylogenetik" (1966a). Er selbst hielt seine „Beiträge zur Morphologie, Ökologie und Phylogenie der Ascaridoidea (Nematoda)" (1958) für die am besten gelungene (siehe Schmitt 1996). Fraglos haben seine populären Bücher über „Die Welt der Parasiten" (1966b), „Evolution" (1972) und „Ökologie" (1973) die größte Breitenwirkung entfaltet.

In den letzten Jahren seiner wissenschaftlichen Betätigung faszinierte ihn zunehmend die Wechselbeziehung zwischen Blüten und ihren Bestäubern, ganz besonders die evolutive Entstehung von Signalen und Täuschungen auf Seiten der Blüten (z. B. 1983).

Günther Osche wurde 2001 die Ehrendoktorwürde der Rheinischen Friedrich-Wilhelms-Universität Bonn verliehen, 2006 wurde er zum Ehrenmitglied der Deutschen Zoologischen Gesellschaft ernannt, deren Präsident er 1973 und 1974 war (s. Sauer 2007).

Wer ihn erlebt hat, weiß, dass noch viel eindrucksvoller als der Autor der Redner Günther Osche war (Fig. 1). In Vorlesungen, Vorträgen und persönlichen Gesprächen hat er seine eigene Begeisterung für die Vielfalt der Organismen und ihrer Leistungen immer wieder auf seine Zuhörer übertragen. Auch wurde er nicht müde seine Bewunderung für August Johann Rösel von Rosenhof, Johann Wolfgang von Goethe und Charles Darwin farbenreich auszudrücken. Er vertrat pointierte Ansichten zu Politik, Erziehung und Ästhetik, an denen sich ohne weiteres lebhafte Diskussionen entzünden konnten. Dabei wurde er nie verletzend, es lag ihm stets an respektvollem Ausgleich. Für diejenigen, die ihm persönlich nahe standen, war er

eine wohlwollende, Vertrauen und Autorität ausstrahlende Vaterfigur. Während der 70er und 80er Jahre des 20. Jahrhunderts prägte er die deutschsprachige Evolutionsbiologie durch seine publizierten Werke ebenso wie durch sein persönliches Auftreten.

Eine kraftvolle Stimme ist verstummt. Wer sie je gehört hat, wird sie immer in sich hören.

Danksagung. Ich danke Gabriele Uhl (Bonn) für die hilfreiche Durchsicht des Manuskripts.

After a short but severe bout of cancer, Prof.Dr.Dr.h.c. Günther Osche passed away on 2nd of February, 2009, in Freiburg im Breisgau, Germany, in the circle of his family. He was born on 7 August 1926, the son of a bank clerk in Haardt near Neustadt an der Weinstrasse, a small town in southwestern Germany. A year after he was born, his parents moved to Nürnberg, where he grew up. He remained true to this town for all his life.

Already as a child and youngster, Günther Osche was an ardent nature lover. All animals interested him, especially birds. At the age of 16 he served in a flak battery, and when he was 17 he was, after an abridged final school examination ("Notabitur"), called into the regular army. In November 1944 he was severely wounded in both legs which remained a lifelong impairment.

Günther Osche studied biology at the University of Erlangen from winter semester, 1946, receiving his doctoral degree in 1951. His dissertation, supervised by Professor Hans-Jürgen Stammer, treated the systematics, phylogeny, and ecology of the genus *Rhabditis* (Nematoda). The same year, he and Elisabeth Riedel married. After his degree, he served as an assistant, earned his habilitation in 1963, and obtained a position as a university docent in Erlangen. In 1967 Günther Osche was appointed full professor of zoology at the Albert Ludwigs-Universität Freiburg im Breisgau. Until his voluntary retirement in 1988 he presented his famous, extensive and rich lecture series on special zoology of the invertebrates for a total of 22 times.

Of his 84 scientific publications, his habilitation thesis on systematic position and phylogeny of the Pentastomida (1963) and his handbook chapter on basics of general phylogenetics (1966a) are especially outstanding. He regarded his contribution on morphology, ecology and phylogeny of the Ascaridoidea (Nematoda) (1958) as his best paper (see SCHMITT 1996). Unquestionably his popular books on the world of parasites (1966b), evolution (1972), and ecology (1973) reached the broadest readership.

During the last years of his professional activity he turned increasingly fascinated by the interaction between flowers and their pollinating insects, especially the evolution of signals and deceptions by plants (e. g. 1983).

In 2001, he was awarded the degree of an honorary doctor by the Rheinische Friedrich Wilhelms-Universität, Bonn, and in 2006 he was elected as an honorary member of the German Zoological Society, of which he was president in 1973 and 1974 (see SAUER 2007).

Whoever met him in lectures and discussions knows that even more impressive than Osche the author was Osche the speaker (Fig. 1). Through lectures, talks and personal conversation, he transferred his own enthusiasm of the multifariousness of organisms and their attributes to his listeners. Tirelessly he expressed in vivid colours his admiration of August Johann Rösel von Rosenhof, Johann Wolfgang von Goethe, and Charles Darwin. He advanced definite views on politics, education, and aesthetics, which easily led to lively discussions. However, he never offended, but always aimed at a fair and respectful balance. To all who were close to him, he was a benevolent fatherly mentor who gave off an air of trustfulness and natural authority. During the seventies and the eighties of the 20th century, he guided evolutionary biology in the German speaking community by his publications, but likewise by his personal performance.

A powerful voice has fallen silent. Whoever has been fortunate to hear it, will hear it forever.

Acknowledgement. I thank Walter J. Bock (New York) for carefully improving the English manuscript.

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KRAFT, R. (2008). Mäuse und Spitzmäuse in Bayern: Verbreitung, Lebensraum, Bestandssituation. 111 S., 63 Farbfotos, 51 Karten, 25 Diagramme, 4 Tabellen. Eugen Ulmer, Stuttgart. ISBN 978-3-8001-5609-2. Preis 39,90 €.

Dieser schmale Band ergänzt das 2004 im gleichen Verlag erschienene Buch „Fledermäuse in Bayern“ (von A. MESCHEDE und B.-U. RUDOLPH). Anders als bei Fledermäusen konnte sich der Autor des vorliegenden Buches weniger auf die Beobachtungen ehrenamtlicher Naturschützer stützen (für Mäuse und Spitzmäuse gibt es keine Lobby), sondern erarbeitete die Daten für die Verbreitungskarten selbst durch langwierige Analyse von Eulengewöllen, die zahlreiche Ornithologen in 332 bayerischen Ortschaften gesammelt hatten. Insgesamt wurden über 40.000 Kleinsäugerbelege durchgesehen und bestimmt. Ergänzend wurde die im Bayerischen Landesamt für Umwelt vorliegenden Daten und Belege aus Museumssammlungen herangezogen. Viel Zeit und Mühe verwendete der Autor auch auf die Anfertigung von Farbfotos lebender Kleinsäuger. Das Resultat ist eine sorgfältig kompilierte Übersicht der für Bayern vorliegenden Kenntnisse von 27 Kleinsäugerarten. Die beigefügten Lebendfotos wird von allem derjenige zu schätzen wissen, der selbst einmal versucht hat, eine Spitzmaus oder eine Waldmaus zu fotografieren. Schade ist, dass nicht alle Arten von Nagern (Biber, Bisam und Nutria fehlen) und Insektenfressern (Igel, Maulwurf) behandelt wurden. Die hier vorgelegten Daten ergänzen unsere Kenntnisse über die Kleinsäugetiere in Deutschland und sind relevant für den Naturschutz in Bayern.

Rainer HUTTERER
Zoologisches Forschungsmuseum Alexander Koenig, Bonn

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Colonisation and Steadyness of Carabid Beetles in Orchards

Jürgen DEUSCHLE & Erich GLÜCK

Abstract. From April 1995 to November 1997 investigations were carried out in the nature reserve "Limburg" (48.36 N/9.23E): data were collected on the type and frequency of grassland use and data on the carabid fauna. 17 sample plots were selected. Part of the plots had 25 years of unchanged management regimes: three-cutting meadows (3), two-cutting meadows (3), mulched meadows (4), abandoned meadows (3), a horse pasture, a sheep pasture with rotational grazing, a continuously grazed sheep pasture, and a sheep pasture abandoned in 1994.

5229 beetles representing 68 carabid species were caught in pitfall traps during the three years of investigation on the 17 study plots (Tab. 2). On nearly all studied areas/plots changed the relative frequency of dominant species. 3-cutting meadows frequently show a one-sided activity dominance structure. Within the yearly spectrum of activity dominance on all areas it is obvious that species occured and are leaving continously.

Rare species in the area (steadyness group I: present on 1–3 plots) reached percentages between 10 % and 42 %, the corresponding values for steadyness group II (species present on 4–6 plots) are 0 % up to 67 % und steadyness group III (present on 7–10 plots) 20 up to 64 % (Fig. 2, Tab. 3). The management of the grass vegetation in orchards and the influence on the carabid community is briefly discussed.

Keywords. Ground beetle, grassland management, species colonisation, species steadyness.

1. INTRODUCTION

Vegetation and fauna of extensively managed orchards are mainly determined by the site and its maintenance, the type of grassland management and its land use intensity (DEUSCHLE et al. 2002, GLÜCK et al. 2004).

Until now animal communities of extensively managed orchards have not been analysed based on the direct comparison of different forms of grassland management There are few investigations dealing with the influence of management systems on arthropod communities in extensively managed grassland, whereas the effects of grazing have been documented more frequently (HANSSEN & HINGST 1995, MAELFAIT et al. 1988, RUSHTON et al. 1989, SCHNITTER 1994, DEUSCHLE & GLÜCK 2001, GLÜCK & DEUSCHLE 2003).

Carabids showed a higher activity on cut and mulched meadows than on plots in state of succession during abandonment trials (SOUTHWOOD & VAN EMDEN 1967). But the abandonment of two meadows, one fertilised and the other one unfertilised, lead to an increase of the activity density during the course of succession (SCHNITTER 1994). Low food resources – determined by differences in a decrease of the population – caused a lower activity density in woodlands (GUILLEMAIN et al. 1997).

Beside describing represent field studies in the last years was tried to explain and scale the differential character of carabid communities. Abiotic and management specific characters and gradients have been worked out. (BAGUETTE 1993, BAUER 1989, BUTTERFIELD & COULSON 1983, DENNIS *et al.* 1997, DUFRENE & LEGENDRE 1997, EYRE *et al.* 1990, HUHTA 1979, LUFF et al. 1992, LUFF 1996, MC FERRAN et al. 1994, MORRIS & RISPIN 1987, PREISZNER 1996, RODE 1993, VOWINKEL 1996, GLÜCK & DEUSCHLE 2003).

The aim of this paper is to ask wether carabids colonize relatively homogenous orchards constantly in nearly the same species and individual densities or in a more stochastic manner, or is there a concentration on some plots/ habitats of specieal species. The species therefore were divided into three classes of steadyness (see 2.2). The constancy in time of the composition of carabid community is inspected and how it is linked up management specific at the background of different management regimes, different area, the distribution with altitude and the shading of the plots. Analysis of similarity of the carabid communities and the activity dominances on the plots show a pattern in time and space of the species compsition and dominance idendities of different management regimes.

2. METHODS

2.1. Census and registration of land use

From the beginning of April until the middle of October 1997 the following parameters were recorded weekly or every two weeks in the study area orchards in the nature reserve "Limburg" (48.38N/9.23E), south west Germany: type of use, time of mowing, "mowing device", "whereabouts" of mowed grass, and number of grazing animals. The amount of ground shaded by trees under perpendicular solar radiation was estimated and assigned to six categories.

All areas, which are mowed completely on a regular basis every year and where the cut grass is removed, will be called "typical meadows". On "mulched meadows" the cut grass remains regardless of the mowing device and mowing frequency. "Continuous grazing" defines the management type of pastures, where the grazing animals can be found permanently on the same area, while "rotational grazing" is the type, where a particular area is being grazed for a period of only a few days, but several times a year. Combinations of the three types of management can also be found in the extensively managed orchards of the nature reserve area.

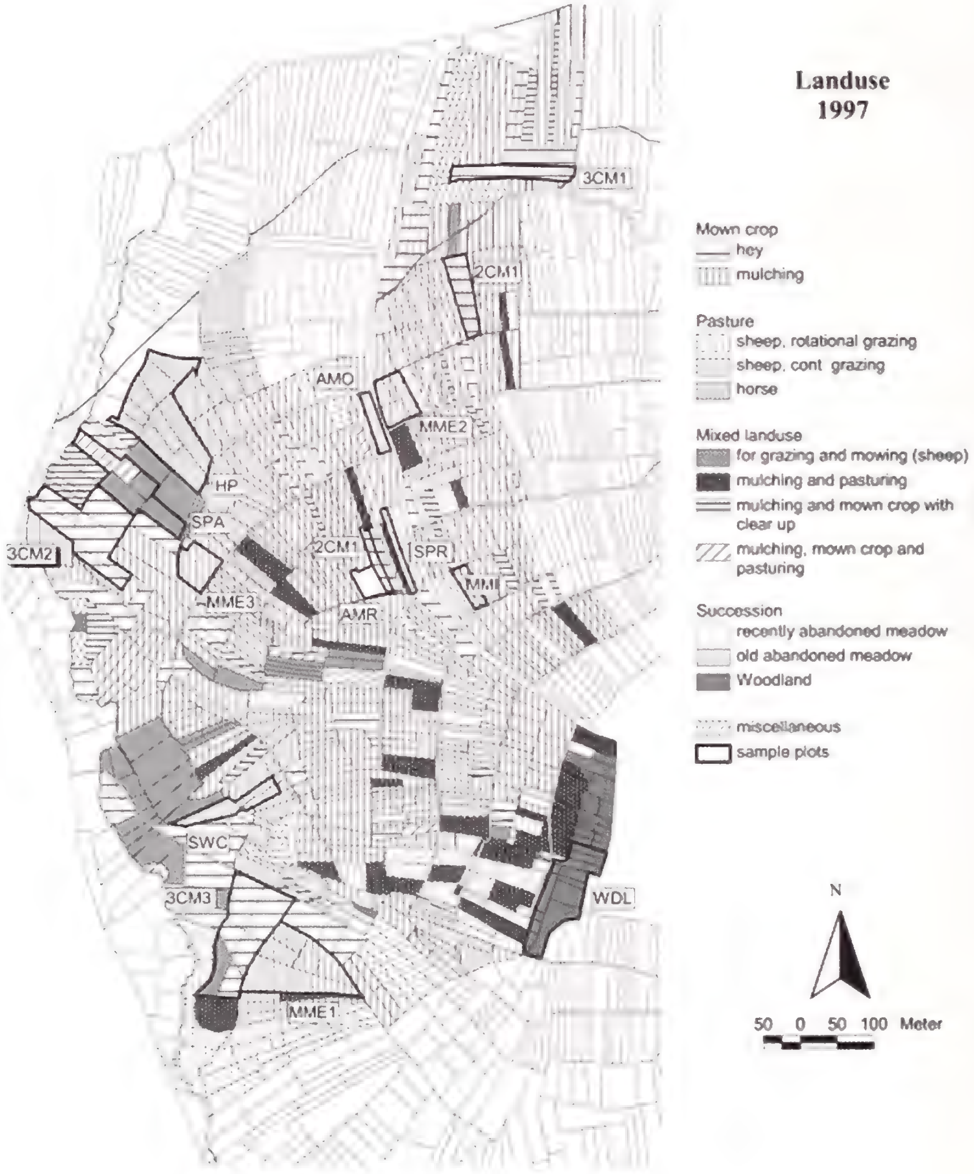
Landuse
1997
3CM1
2CM1
AMO
MME2
HP
SPA
3CM2
2CM1
SPR
MMI
MME3
AMR
SWC
3CM3
WDL
MME1
Mown crop
hey
mulching
Pasture
sheep, rotational grazing
sheep, cont grazing
horse
Mixed landuse
for grazing and mowing (sheep)
mulching and pasturing
mulching and mown crop with clear up
mulching, mown crop and pasturing
Succession
recently abandoned meadow
old abandoned meadow
Woodland
miscellaneous
sample plots
N
50 0 50 100 Meter

Fig. 1. Land use intensity of grassland in the study area during the vegetation period of 1997 and the sample plots.

2.2. Selection of sample plots and Population census

In 1995 the selection of sample plots took into consideration areas which had been under the same management system for more than 25 years (see Fig.1, Tab. 1).

Six pitfall traps were placed in a single line 10 m apart as a transect through the centre of each sampling plot. Ethylene glycol (50 %) was used as preservative solution, with detergent added to reduce surface tension. A cover made of Perspex (120 by 120 mm) was installed 30–50 mm above ground level. In 1995 (5. April to 1. November) traps were controlled and emptied regularly weekly. In 1996 (5. May to 4. November) and 1997 (8. April to 4. November) the control interval was two weeks (Deuschle & Glück 2001).

The division in classes of steadyness helps to classify the rareness in the study area, independent from their plot specific frequency, where ever this scarcity is only valuable for the individual study plots. The species were divided into three classes of steadyness: steadyness I are all species occuring on 1–3 plots, steadyness II species occuring on 4–6 plots, steadyness III species occuring on 7–9 plots.

2.3. Analysis of data and statistical methods

All registered data concerning management practices, vegetation, soil condition, and carabid population were integrated into a database. After examining the necessary conditions the following statistical tests were applied: U-test by Mann & Whitney (MWU-test), and X^2-test. The rank correlation was calculated according to Spearman and the coefficients were tested on their significance.

3. RESULTS

3.1. Acitivity dominance

The activity density of carabids on the various plots is quite different (Tab 2). The yearly activity density on the three fold mowed meadow (3CM1) showed differences in the distribution of the second up to the fifth dominant species. The percentages of these species (*Amara aenea, Pseudoophonus rufipes, and Nebria brevicollis*) decrease continually within the three year study. In 1995 *P. rufipes* and *N. brevicollis* were the third respective fifth dominant species an 1997 both were totally absent. In contrast to this the percentages of *Clivina fossor, Poecilus cupreus*, and *Carabus ullrichi* steadily increase throughput the three year period. Only *Anisodactylus binotatus* in all three years remained as the cominant species despite of its changing perdentages in the area. Six species occured 1995 in a low density, they were absent in 1996 and occured again in low density 1997. In 1996 and 1997 seven species are registered which were not collected in 1995 in the pitfall traps, two of the species were captured only in 1996, and three species out of them in 1997. On the 2-cutting meadow (2CM1) the dominant species changed during the three years of investigation: *Harpalus latus,* the activity of which decreased countinously is removed by *C. ullrichi* the percentage of which increased. The next following species hold nearly the same dominance ranks with the years. Three species are only in 1995 and 1997, seven species only in 1995 registered. Eight more species are only present in 1996 and 1997, two out of them only in 1997.

On the horse pasture (HP) all years the dominance of species changes from *C. fossor* to *Pterostichus vernalis* on to *Pterostichus melanarius*, the percentage of the latter increased from 1% in 1995 to 8.5% up to 29.1% in 1997. The percentages of the other dominant species decrease with the years. *A. plebeja* is registered only in 1995; *Amara familiaris* and *C. ullrichi* restricted their occurance in 1995 and 1997 also on this plot. In contrast in 1996 new species occured in the community, six more species in 1997 by most of them only one individual was collected.

On the anbandoned sheep pasture (SPA) *P. melanarius* remains as the most dominant speacies and reached eudominant status, with 39,4 % in 1995 and 58,4 % in 1997. *N. brevicollis* disappeared on this plot in 1997. This species ranked in 1995 still on the second dominance position. Three species were registered exclusive on this plot in 1995, five only in 1996 and six species only in 1997.

On the sheep pasture rotational grazing (SPR) *C. ullrichi* was the most dominant species througout the three years. *Pterostichus ovoideus* strongly increased and was collected in the same frequency as *C. ullrichi*. On this plot four species occured only in 1995 or 1996, five more occured only in 1997.

On the mulched meadow (MMI) *Leistus ferrugineus* removed the so far most frequent *C. fossor* 1997. *L. ferrugineus* occured the first time in this community, reached a percentage of 6,1 % and is ordered in status to the subdominant carabids. The percentages of species belonging to the dominant ones in 1995 changed strongly and are displaced by the so far subdominant species as *C. ullrichi*. Seven species are trapped only in 1995, ten more species in 1996 and 1997 four out of these only in one of both years.

The dominance spectrum is wellbalanced on the mulched meadow (MME2). *H. latus* reaches all the years' eudominant status. Three species are registered only in 1995, two more in 1996 and no more in 1997.

Table 1. Morphology and land use of sampled plots.

Plot	Land use	Type of land use	Area (Ar)	Circumference (m)	Altitude (mNN)	Shading (%)	Sampling period
3CM2	3-cutting meadow	Meadow	26	209	405	20	`97
3CM3	3-cutting meadow	Meadow	51	287	425	20	`97
3CM1	3-cutting meadow	Meadow	16	204	392	20	´95,´96,`97
2CM3	2-cutting meadow	Meadow	40	446	415	80	`97
2CM1	2-cutting meadow	Meadow	10	218	445	60	´95,´96,`97
2CM2	2-cutting meadow	Meadow	15	250	410	60	`97
SPA	abandoned sheep pasture (continuous grazing), see text	Pasture	34	234	405	60	´95,´96,`97
SPC	Sheep pasture (continuous grazing)	Pasture	15	213	415	80	`97
HP	Horse pasture	Pasture	124	580	400	20	´95,´96,`97
SPR	Sheep pasture (rotational grazing)	Pasture	11	259	445	20	´95,´96,`97
MMI	Mulched meadow (4 - 6 cuttings)	Mulched meadow	12	162	455	20	´95,´96,`97
MME1	Mulched meadow (3 cuttings)	Mulched meadow	47	380	440	100	`97
MME2	Mulched meadow (2 – 3 cuttings)	Mulched meadow	29	217	420	60	´95,´96,`97
MME3	Mulched meadow with 1 cutting	Mulched meadow	25	206	517	80	`97
AMR	Recently abandoned meadow (4 years)	Succession	13	153	445	0	´95,´96,`97
AMO	Old abandoned meadow (10 years)	Succession	13	202	420	100	´95,´96,`97
WDL	Woodland	Succession	13	222	520	100	`97

On the recently abandoned meadow (AMR) *H. latus* displaced 1996 the so far most frequent *A. binotatus*, the latter belonged in 1996 and 1997 just to the group of subdominant species.

The percentages the persuiting dominant species on the plot *P. ovoideus*, *C. fossor* and *Bembidion obtusum* changed strongly during the years. Four species are registered only 1995, six more only in 1996 and 1997.

In the dominance spectrum of the old abandoned meadow (AMO) set apart from the percentages of the most frequent and dominant species from year to year considerably and lead to a yearly change in the ranking of the community, during the course1996 and 1997 only few species added new into the community.

Spectrum and the ranking of dominant and subdominant of species change strongly within the study plots and years. Regarding comparative management forms there are great differences regarding the main species in the spectrum (Tab. 2).

The percentage of the most frequent species compared to the number of all species together did not show any connection with the number of species or individuals nor the management of the plots. The maximal and minimal values are given on three year investigated plots on the abandoned sheep pasture (SPA, 58,4 %) in 1997 and on the horse pasture (HP, 13,9 %) 1996).

On the one year investigated plots owns the 3-cutting meadow (3CM3) with 16,4 % the lowest value , the like-

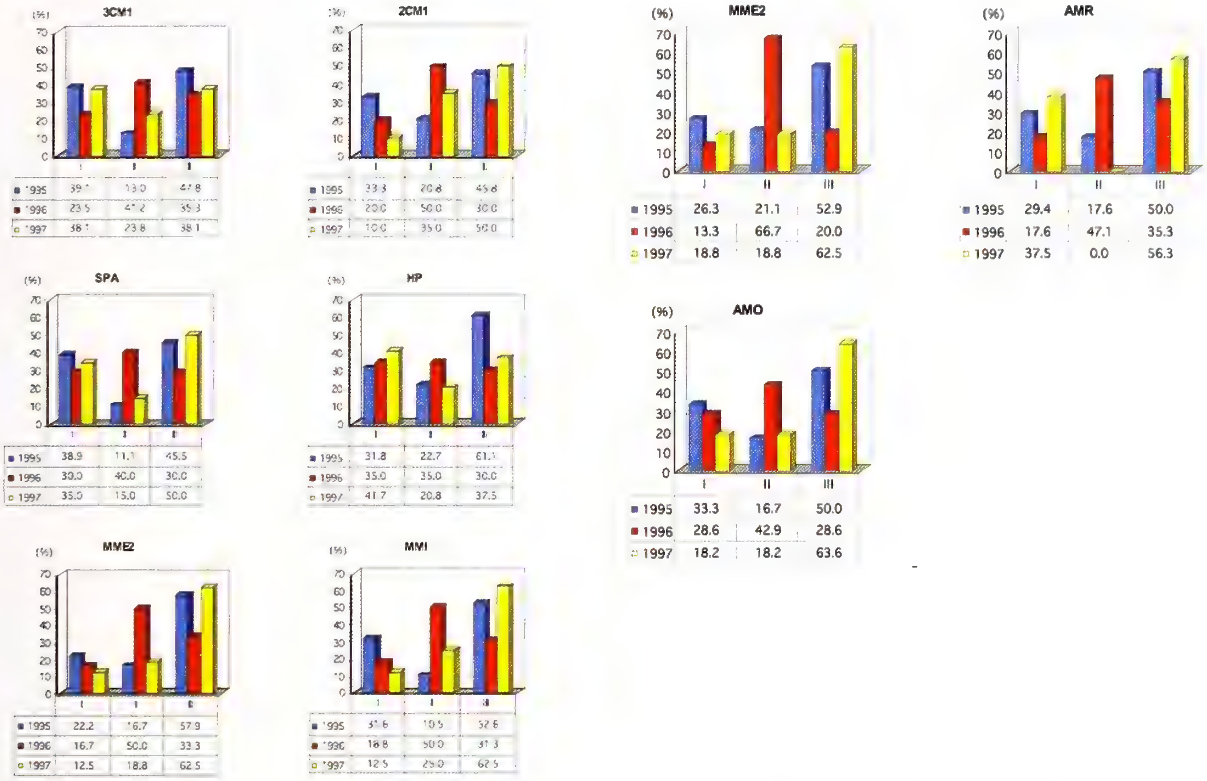

Fig. 2. Steadyness of carabid species from 1995–1997 on plots of different management 3CM1, 2CM1, SPA, HP, MME2 and MMI (left) / MME2, AMR and AMO (right) (species percentages).

wise 3-cutting meadow (3CM3) with 49,4 the highest value. Eleven different species built up the most frequent carabid on the three year investigated plots; *H. latus* was for seven times the most frequent on the nine investigated plots. Only on the areas 3CM1, MME2 and SPA in all three years the same species reach the highest frequency (*A. binotatus, H. latus* and *C. ullrichi*). From the other species are *C. ullrichi, C. fossor, A. binotatus, P. vernalis* und *P. ovoideus* high steady and occur on nearly all other plots. *P. melanarius* und *A. parallelepipedus* are registered only on a few investigated plots. The arrangement of the most frequent and second most frequent species does not show any affinity to compatible or to near by standing management forms.

3.2. Steadyness of species on the plots

The determined steadyness allows on the three year studied areas/plots a differentiation between three groups. The first group consists of species which colonize regularily two-third of the study plots (Steadyness III, Fig. 2). This group comprises 1995: 11 (24 %) of altogether 46 species, 1996: 6 (15 %) from 39 species and 1997: 10 from 38 (26 %) species. The second group (steadyness II) comprises 1995: 8 (17 %), 1996: 14 (36 %) und 1997: 7 (18 %) of the species. The third group comprises the large part of all detectable species (Steadyness I). 27 (59 %) of the species 1995 contained in the pitfall traps were only present on one to three study areas/plots. In 1996 19 (49 %) species belonged to this group, 1997: 21 (55 %). With this the percentages of the classes of steadyness in 1995 und 1997 are comparable. 1996 evidence of some rare species in the study area/plots are absent (probably dependent on the low activity). In 1995 more frequent species are detected on less study plots, so in 1996 the steadyness class II was comparatively high occupied (Fig. 2).

The highest proportions of steadyness I were registered on the 3-cutting meadow (3CM1) and on the abandoned sheep pasture (SPA) (39 %), the lowest percentages of this class were in the carabid community on the plot 2CM1 (1997: 10 %, Fig. 2). The percentages on the plots are between 7 % (MME2) and 23 % (2CM2), beside the horse pasture (HP) the values are in 1996 negligible lower compared to 1995 oder 1997.

Some of this rare species in the study area are able to establish in seperate years or continously on distinct plots larger populations. To this species belong *Abax parallelepipedus*, *Amara aenea*, *Bembidion properans* or *Pterostichus melanarius*.

Table 2. Density of species, activity abundance, dominance index, area specific proportions of main and accessory species and the most frequent species each in the perennial sample plots (1995–1997).

Area:		**3CM1**	**2CM1**	**SPA**	**HP**	**SPR**	**MMI**	**MME2**	**AMR**	**AMO**
Number of species	1995	23	24	18	22	18	19	19	17	12
	1996	17	20	20	20	18	16	15	17	7
	1997	21	20	20	24	16	16	16	16	11
Number of individuals:	1995	226	144	226	200	76	95	86	84	81
	1996	64	58	81	130	69	49	41	82	56
	1997	125	75	267	234	87	106	113	60	58
Percentage of Main species: (%)	1995	26,1	31,8	27,8	36,4	55,6	42,1	52,6	41,2	66,7
	1996	58,8	65,0	35,0	45,0	50,0	56,3	66,7	41,2	85,7
	1997	42,9	50,0	25,0	37,5	62,5	62,5	31,3	50,0	72,7
Percentage of Accessory sp.: (%)	1995	73,9	68,2	72,2	63,6	44,4	57,9	47,4	58,8	33,3
	1996	41,2	35,0	65,0	55,0	50,0	43,8	33,3	58,3	14,3
	1997	57,1	50	75,0	62,5	37,5	37,5	68,8	50,0	27,3
dominance index (%):	1995	25,5	31,3	39,4	18,0	31,6	33,7	29,1	16,7	37
	1996	15,6	22,4	25,9	13,9	18,8	18,4	29,3	24,4	48,2
	1997	31,2	21,3	58,4	29,1	18,4	19,8	28,3	30,0	24,1
Most frequent species:	1995	*Anisod. binotatus*	*Harpalus latus*	*Pt. melanarius*	*Clivina fossor*	*Carabus ullrichi*	*Clivina fossor*	*Harpalus latus*	*Anisod. binotat.*	*A.parallelepipedus*
	1996	*Anisod. binotatus*	*Harpalus latus*	*Pt. melanarius*	*Pt. vernalis*	*Carabus ullrichi*	*Clivina fossor*	*Harpalus latus*	*Harpalus. latus*	*Molops elatus*
	1997	*Anisod. binotatus*	*Carabus ullrichi*	*Pt. melanarius*	*Pt. melanarius*	*C. ullrichi/ Pt. ovoideus*	*L. ferrugineus*	*Harpalus latus*	*Harpalus. latus*	*A.parallelus /Harpalus latus*

The area specific percentages in class II stagger between 0 % (AMR 1997) und 50 % (SPR, MMI 1996). The scattering on the plots within the 3 year study is essentially higher in this class of steadyness I, the values are beween 14 % (HP) und 47 % (AMR).

Species of steadyness III colonized all study plots/areas. The highest percentages in this class are on AMO (64 %) und MME2 (63 %) in1997. On the same areas are the lowest percentages in 1996 (29 % bzw. 20 %). The area specific percentages of the community stagger considerably (13–43 %).

The unequivocal distribution of the steadynes shows clear, that within the relatively homogeous and enclosed orchards in the study area exist numerous small-patterned differences which can lead to inhomogenous distributions on neughbouring areas. A smaller part of species colonizes the orchards in changing frequencies nearly overall. The majority of species concentrate abviously only on small-patterned and local distribution centres, Their discontinually and recedental occurance in other areas allows the interpretation that ther behaviour is a navigational exploration.

1996 and 1997 the percentage of rare species (steadyness I) increased with increasing area of the plots, 1997 the correlation was statistically significant (Tab. 3). In the three years of investigation the percentage descreased with increasing altitude, the correlation in 1997 was statistically significant.

The steadyness seems not to be correlated with the parameters of the plots like management, circumference and shading; the correlation analysis did not show any tendencies. Only 1997 the percentage of frequent species (steadyness III) increased with decreasing management intensitymit, 1996 the percentage decreased statistically signif-

Table 3. Rank correlation coefficient of species percentages of different steadyness classes of the carabid community with area parameters (n = 9; level of significance: * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

	Species percentages	Management	Area	circumference	altitude	shading
1995	SC I	-0.56	0.28	-0.01	-0.59	0.33
	SC II	0.12	0.19	0.36	-0.18	0.03
	SC III	0.38	0.13	0.27	0.11	-0.34
1996	SC I	-0.35	0.52	0.32	-0.60	0.22
	SC II	0.31	-0.63	-0.27	0.70*	0.09
	SC III	-0.28	-0.32	-0.26	0.13	-0.84**
1997	SC I	-0.11	0.81**	0.08	-0.76*	-0.37
	SC II	-0.55	-0.34	0.16	0.12	0.01
	SC III	0.77*	-0.40	-0.43	0.57	0.34

icant with increasing shading. So that seems between the comparatively rich species mowing meadows and pastures and the scarce species areas like abandoned and mulching meadows are no differences in the percentages of rarely or frequent species in the sudy area (Tab. 3).

In contrast the percentages of rare species (steadyness I) increase with increasing area 1996 and 1997, 1997 the correlation was statistically significant. In all three years the percentage of these species decreased with increasing altitude of the study plots.

4. DISCUSSION

Three cutting meadows are colonized by numerous species, which occur either in a high population density and/or are not present on other areas. The typical speceis on three cutting meadows are predominantly spreeding and euritopic forms, which colonize a broad spectrum of different habitats. Some of this species, as *P. melanarius* or *C. fossor* indicate with high population densities intensive management forms (Desender *et al.* 1994, Tietze 1985, 1987).

The species colonizing 3-cutting meadows belong mostly to steadyness III or I, but seldom to II. They are therefore either high frequent or very rare. In four of these species the individual density was significantly higher than on other study areas, on which they occured regularily in scarce populations (Tab. 2). These species belong mostly to steadyness III (*A. binotatus*, *P. cupreus*, *C. fossor*, exception: *Pt. melanarius*). *A. binotatus, P. cupreus* and *C. fossor* colonized all 3-cutting meadows continously and therefore in time and space on all areas of this management form present. All four species are capable to fly, two species are macropteric and two are alae dimorphic and therefore comparable mobil. However from *P. melanarius* and *C. fossor* no completely macropteric individuals were registered. Especially *P. melanarius* colonized the area 3CM2 and 3CM3 as well as the neighboured pastures in high population densities but was absent on 3CM1 (Desender *et al.* 1994). Obviously in its spreading pattern seems to be content an area dependent gradient, which had not been jet registered: in the sout-western part of the study area the species occured 1997 on nearly all studied plots therby also on pessimissm areas (MME3). In the north-eastern part of the area there are only some lonely individuals captured (1996: SPR, 1997: AMR) and in our opinion optimal areas (3CM1) have not been colonized. Large 3-cutting meadows and pastures are common in the south-eastern part of the study area, wheras they are on the remaining area more rare and smaller and mostly surrounded by mulching meadows. (Fig.1). The unability to fly and therefore beeing scarcely mobile in the investigated populations seems potentially more favorable colonizing, but prevents colonizing of secluded mowing meadows in other parts of the study area. Therefore the species overall distribution is not only based on suitable management forms or habitats but also on the attainment of exploring individuals of local populations, which depends on the species immanent mobility. With more typical species of 3-cutting meadows the density of individuals are clear lower, they colonize the plots with other management forms essentially more rare and fall mostly in steadyness class I. (*Amara aenea, Bembidion properans, Agonum mülleri, Poecilus versicolor, Carabus granulatus, Diachromus germanus, Amara montivaga).* Except *C. granulatus* (brachypteric), all individuals of the species are macropteric. They are therfore capable to fly and more mobil in contrast to the differential species of stedyness group III. In contrast to the differentiating species from steadyness group I on the studied 3-cutting meadows they are less continously present in time and space. This discontinous presence and the lower population density indicates a lower plasticity and a higher risk of extinction in local populations of this species, whereas eurytopic species with high plasticity even are able to colonize pessimal areas. For the latter therefore seems the ability to fly of reduced importance.

Some of the differential species on 3-cutting meadows (especially of steadyness group III) colonize pastures more frequently. These are *P. melanarius* and *P. vernalis* which colonize both management forms in higher populations densities than 2-cutting meadows, mulching or abandoned meadows. They mark the similarity of the carbid community of both management forms which obviously represent comparable living conditions. Species colonizing only pastures in high densely populations were only present by *Pt. macer* und *P. rufipes*. Their rarely population densities did not allow to mark off statistically signifcance to other management forms. (Fig. 2).

N. brevicollis and *C. ullrichi* have been trapped significantly more frequent on 2-cutting meadows compared to other management forms. Both species are counted to the more frequent ones (steadyness II / steadyness III) and colonize all other management forms at least in low densities (Fig. 2). But both species dave been very frequent on the area 2CM3 out of the direct Limburg area, and hint the first time an influence independent from the management form on the composition of specific carbid communities in orchards. The eurytopic *N. brevicollis* is a typical species of the woodland edge (THIELE 1964). Their densely population on 2-cutting meadows and scarce activity on abandoned areas is different from this findings, but a overall high presence on the study plots confirms the morphological relationship from orchards and thin woodlands. Both habitats offer obviously for *N. brevicollis* comparable living conditions (see GRUSCHWITZ 1983). After the scarce specifications, the rarely found species *C. ullrichi* (RL 3) inhabits a broad spectrum of various habitats with ist centre of distribution in Southern Europe. The statements are from loamy fields, meadows, and rural areas up to thin woodlands (HŮRKA 1996).This plasticity seems to correspond to the high steady presence on all studied plots.

Leistus ferrugineus, the only species with its centre of distribution in mulching meadows increased rapidly over the three year study (1995: steadyness I, 1996: II, 1997: III). In contrast euritopic species of abandoned meadows (*Carabus auratus, Abax parallelus, Abax parallelepipedus*) are more often present on meadows and pastures. *A. parallelus* (1995 – 1997: steadyness II) is more common than *A. parallelepipedus* (1995, 1997: steadyness I, 1996: II) and reaches moreover a higher population density on mulching meadows. *A. parallelus* therefore is the species with higher plasticity and a lower bonding to cultivating or succession phases. So called stenotopic woodland species however are in extensive orchards restricted on succession areas or border on woodlands (*M. elatus, C. coriaceus, C. nemoralis*). They indicate thereby a strong change of the carabid community on a complete abandonment.

Beside the differential species there are obviously some highly steady species (steadyness III), which colonize all studied plots in nearly the same density, whenever it is remarquable that they also reflect a specific tendency of cultivation. *H. latus* (macropteric) colonizes on less nutrient cutting meadows and pastures in a slightly higher density than on mulching meadows and abandoned meadows. Its centre of distribution in the grassland remains more likely on ologotrophic areas (TIETZE 1985, Fig. 2).

Pt. ovoideus (brachypteric), colonises 2-cutting meadows, mulching meadows und abandoned meadows more frequently.

The area specific percentages of the steadyness groups I–III are obviously not influenced by the management form of the study plots. On the species rich cutting meadows and pastures especially rare species are not found more frequent compared to low species areas as mulching meadows and abandoned meadows. But the area specific percentages of steadyness group I decrease tendentious with decreasing size and increasing altitude of the plots. For larger plots are more frequent at the bottom of the "Limburg" area, and therefore at the border of the study area, the higher percentage of rare species on this plots can be true to influences of the surrounding areas. This influence became scarcer – regarding overall influences – with increasing distance of the studied plots from the border in the centre of the "Limburg" area.

5. ZUSAMMENFASSUNG

Von April 1995 bis November 1997 wurden in den Streuobstwiesen des Naturschutzgebietes Limburg bei Weilheim/Teck (48.38 N/9.23 E) auf einer Fläche von etwa 62,7 ha (857 Flurstücke, Abb. 1) Kartierungen, Erfassungen und Messungen der Grünlandnutzung und –häufigkeit, Vegetation und Carabidenfauna durchgeführt. Dabei wurden 17 Probeflächen mit einem teilweise seit über 25 Jahren unveränderten spezifischen Management ausgewählt. Nutzungsformen waren: dreischürige Mähwiesen (3), zweischürige Mähwiesen (3), Mulchwiesen (4), Sukzessionsflächen (3), eine Pferdeweide, eine Schaf-Standweide, eine Schaf-Umtriebsweide und eine 1994 aufgelassene Schaf-Standweide.

Im Gebiet der 17 Probeflächen wurden insgesamt 68 Species registriert (Tab. 2). Auf annähernd allen Flächen wechselte in den einzelenen Jahren die relative Häufigkeit der dominanten Spezies. Dreischürige Mähwiesen besitzen häufig eine einseitige Dominanzstruktur. Innerhalb der järlichen Spektren der Aktivitätsdominanz wurden auf allen Flächen kontinuierlich Neuzugänge und Abgänge registriert.

Im Areal seltene Species (Stetigkeitsklasse I: auf 1–3 Flächen präsent) besaßen Anteile zwischen 10 % und 42 %, die entsprechenden Werte für Stetigkeitsklasse II (auf 4–6 Flächen präsent) betrugen 0 % und 67 % und für Stetigkeitsklasse III (auf 7–10 Flächen präsent) 20 und 64 % (Abb. 2, Tab. 3). Die Bewirtschaftung des Unterwuchses von Streuobstwiesen hinsichtlich der Beeinflussung der Zönosen wird diskutiert.

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Ten Instars in the Leprous Grasshopper, *Phymateus leprosus* (Fabricius, 1793) (Caelifera: Pyrgomorphidae): Maximum Number Recorded in the Acridoidea

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Abstract. First instars of the pyrgomorphid *Phymateus leprosus* (Fabricius, 1793) were collected in the Great Karoo (South Africa). In the field about 190 hoppers were distributed in small groups over 1.5 m^2 during the day, but densely aggregated during the night. The hoppers reared in captivity, were fed with *Vincetoxicum*, *Euphorbia* and *Rubus*. The mortality of the first instar hoppers was 97 %, but few of those that survived reached adult moult. Ten juvenile instars of variable duration (2–8 weeks each) occurred in both sexes, which is the highest known stage number in the Acridoidea. Postfemur and body length measurements (exuviae) as well as short descriptions are presented for each instar. The juvenile development lasted about one year, and the phenology corresponded with long-standing field observations by Bishop (1940). One male and three female grasshoppers completed the biennial life cycle (April 2000 to January 2002). The adult lifespan amounted to 2–8 months, with mating attempts after three months, but no egg pods were produced. The ovariole numbers varied from 116 to more than 187. Fully developed eggs were found in females that died in July/August, but not in a female that died the following January. The few known reproduction parameters of the genus *Phymateus* are summarized.

Keywords. *Phymateus*, juvenile stages, biennial life cycle, reproduction, South Africa.

1. INTRODUCTION

The genus *Phymateus* belongs to the tribe Phymateini within the family Pyrgomorphidae (Kevan & Akbar 1964). It is distributed with eight species in continental Africa south of the Sahara and two species in Madagascar (distribution maps in Anonymous 1982). These giant and colourful Orthoptera are popularly known as bush grasshoppers or bushhoppers, sometimes (and erroneously) as bush locusts or milkweed locusts. They inhabit semideserts with Karoo vegetation, tree savannas, woodland, as well as gardens and other cultivated areas (Anonymous 1982, Johnsen 1990, Picker et al. 2002). They can cause damage in several crops (summarized by Uvarov 1977, Anonymous 1982, Sithole 1986). This initiated studies on their biology, dealing with life cycles (Bishop 1940, De Lotto 1951), food habits (Kevan 1949, Chapman 1962), and hopper behaviour (Roffey 1964, Rowell 1967). The chemical defence of the pyrgomorphids including *Phymateus* was summarized by Whitman (1990). Recently, the genus became a study object in biochemical and endocrinological research (e.g. Gäde & Kellner 1995, Gäde 2002), pharmacophagy (Seibt et al. 2000), and flight capability (Kutsch et al. 2002). Ephemeral studies dealt with local dispersion, thermoregulation, and short-term movement of adult bush grasshoppers (Köhler et al. 1999, 2001a). Despite of these research activities, few data exist about the complete life cycle in either the field or the laboratory. Information on hopper stages are available from only two *Phymateus* species (Bishop 1940, De Lotto 1951, Kaufmann 2000). Therefore, the present article focuses on the instars of *Phymateus leprosus* (Fabricius, 1793), particularly their number, morphometry and duration. The species, here popularly named as leprous grasshopper (according to Samways 2005), was reared over its whole life cycle in the laboratory, enabling us for the first time to observe an exact number and differences of the instars.

2. MATERIAL AND METHODS

In the afternoon of the 24th April 2000 a bulk of densely aggregated hatchlings of *P. leprosus* was found in the Eastern Great Karoo, South Africa, about 100 km N Port Elizabeth near a camp with typical Karoo vegetation (S.R.). With respect to an ovariole number >200 per female (see Table 2) and the same size and colour of hoppers within the bulk, it was very likely the complete offspring of one egg pod deposited nearby in the soil, but which was not found. Most of the hoppers were collected next morning in a plastic contain and, together with some not specified native plant species, transported to Jena/Germany. Later the adults were identified as *Phymateus leprosus* (Fabricius, 1793).

About one week after collection the hoppers were reared in a terrarium (l 34 x w 18 x h 46 cm) in the Institute of Ecology (G.K.), placed on the sunny window directed to SSE. During field-work in the Great Karoo the adults of *P. leprosus* were mostly found on *Asclepias* bushes (KÖHLER 1999, 2001a). And BISHOP (1940) mentioned a frequently attacked *Euphorbia* species. Therefore we offered food plants of the same families, *Vincetoxicum hirundinaria* (Asclepiadaceae) and *Euphorbia cyparissias* (Euphorbiaceae), from the surroundings of Jena from May to October 2000. Because these plants were not available in winter of 2000/2001, leaves of *Rubus* sp. (Rosaceae), a generally accepted food plant for herbivorous insects, were provided during further captivity. According to ANONYMOUS (1982) and our field observations grass is not eaten by the species.

In regular intervals the exuviae of the hoppers were collected and preserved dry. Later the length of the left hind femur and the body length from these exuviae were measured with an Electronic Vernier Calliper (Helios-digit, accuracy 0.02 mm). The formation of wing pads was noted. For measuring the early instars a stereoscope (x10) was used. The exuviae of all instars are deposited in the Institute of Ecology at the University of Jena. The culture was maintained until the death of the last adult. Immediately after death, the females were dissected for classifying the ovarian development according to the terminology (I–IV) of PHIPPS (1949) and for counting the ovarioles resp. eggs.

Later the preserved and mounted adults were also measured (body length, pronotum, postfemur, forewing). For not stressing the few individuals, no photos or line drawings were made. The sex ratio was determined from the dead first instar hoppers, and from those that survived. To do this, the hardened hoppers were softened with water vapour. Despite the black colouration the sex of most individuals was identified by the shape of the external genitalia of the terminal abdominal segments (subgenital plate in male, upper and lower ovipositor valves in female – as described in UVAROV 1966).

3. RESULTS

3.1. Offspring, mortality, and hopper aggregation

From the aggregated bulk in the field (Fig. 1), altogether 172 first instar hoppers had been sampled, whereas about 5–10 % had escaped. Thus, about 180–190 hoppers should have hatched from this obviously one egg pod. The sex ratio of the bulk could be confirmed as nearly equal, with altogether 84 male and 80 female first instar hoppers, and 8 of unknown sex. These first instar hoppers suffered from a very high mortality, perhaps to a lower extent by the transport stress and after that mainly by the habituation to new food plants in the culture (*Vincetoxicum, Euphorbia*). Otherwise, from the potential native food plants given into the plastic contain only few were eaten during the transport. After one week of transport, 30 dead hoppers were found in the plastic contain, resulting in a mortality of 17 %. During the following two weeks in the terrarium nearly all individuals of the surviving bulk also died, so the total first instar mortality amounted to 97 %. Only five hoppers moulted in early May to the second instar, but these five survived to adult moult, with *Vincetoxicum, Euphorbia* and *Rubus* as food plants.

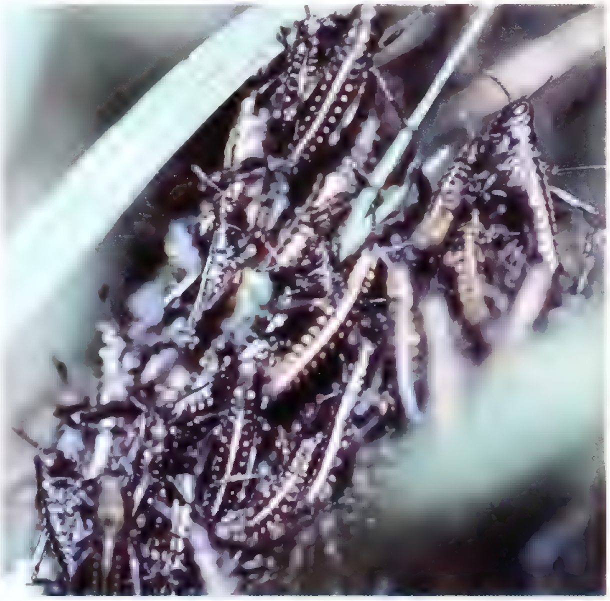

Fig. 1. Bulk of first instar hoppers of *Phymateus leprosus* (body size about 6 mm) showing aggregation behaviour in the late afternoon. Eastern Great Karoo, South Africa, late April 2000. Photo: S. Roth.

The field observations in the Karoo showed that in the afternoon (24.04.2000, about 20°C, some clouds) the individuals were distributed over an area of about 1.5 m^2 mostly in small groups of five to ten hatchlings sitting at a height of 30–40 cm on high shrubs and grasses. With decreasing evening temperature and during the relatively chilly night (8–10 °C) all individuals gathered into a single dense bulk occupying about 0.15 m in diameter (Fig. 1). The aggregation behaviour was also observed in the following days within the plastic contain: dense aggregations during the night and looser ones during the day.

3.2. Number, colouration and duration of instars

Both hind femur and body length of exuviae originating from successive moults showed ten size classes with al-

Table 1. Morphometrical parameters of all developmental stages of *Phymateus leprosus* (Fabricius). Measurements: in juveniles – exuviae, in adults – dry mounted specimens. One male and four (juv.) resp. three females (ad.). In brackets – length influenced by shrinkage.

Parameter	**Postfemur length (mm)**		**Body length (mm)**	
instar / sex	**male**	**female**	**male**	**female**
1	2.9	2.9–3.0	6.8	6.2–6.7
2	3.9	3.9–4.3	8.4	7.1–8.0
3	5.0	4.7–5.0	10.1	8.8–9.6
4	5.8	5.8–6.6	10.7	10.2–11.8
5	7.4	7.3–8.3	12.7	11.8–13.7
6	9.0	8.5–10.7	16.0	13.8–16.1
7	11.5	10.9–13.2	[15.5]	16.8–17.8
8	14.9	13.1–16.4	19.1	20.1–25.1
9	17.7	18.1–19.7	24.9	27.1–34.7
10	23.3	23.1–25.8	42.8	42.5–42.8
adult	30.0	30.0–33.0	[50.0]	58.0–62.0

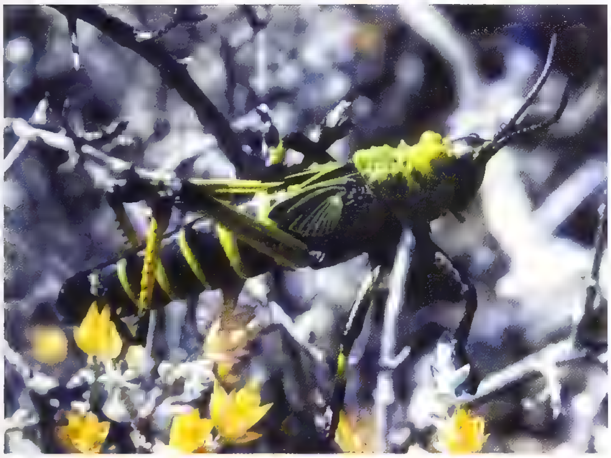

Fig. 2. Last instar nymph of *Phymateus leprosus* (body size about 40 mm). Great Karoo (S.A.), Tierberg Research Centre. Photo: J. Samietz.

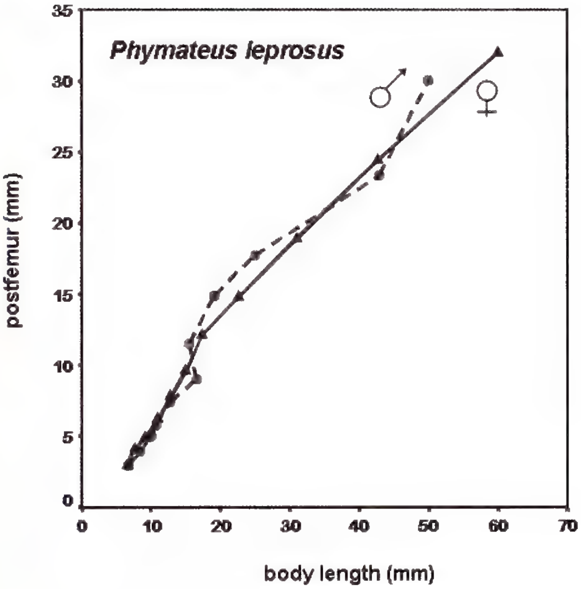

Fig. 3. Isometric growth in juvenile development of both sexes in *Phymateus leprosus*. Male (n = 1), females (n = 3). See also Table 1.

most no overlap in the male and females of *P. leprosus* (Table 1). According to the location of the wing pads, there are eight hopper (L1–L8) and two nymphal stages (L9–L10; Fig. 2). There is an isometric growth between body and postfemur length (Fig. 3). The body size of both sexes was largely identical over the entire juvenile development, but showed considerable differences in the adult stage (Table 1, Fig. 3).

The instars one to three were mostly black with several small yellowish or orange markings (Fig. 1). Two light spots were on the frons. On the upper and lateral pronotum as well as along the margins there were yellowish markings. On each of the first eight abdominal segments there was a lateral drop-shaped to trapezoid spot, whereas dorsally a fine creamy stripe occurred. Ventrally the thorax had four lateral spots near the coxae of the first and third pair of legs, while the antenna and legs were completely black. In the female hoppers the markings appeared slightly larger than in the male hoppers. Beginning with instar four the lighter portions (more or less of a bright green) extended successively, beginning on the tibiae of the hind and median legs, followed by the pronotum and other parts of the body (Fig. 2). In both sexes, the antennal segments increased from eight (instar 1–4) over eleven (instar 5–6) and 15 (instar 7) to 18–20 (instar 8–9) and 21 (instar 10 – Fig. 2), and in the females they varied

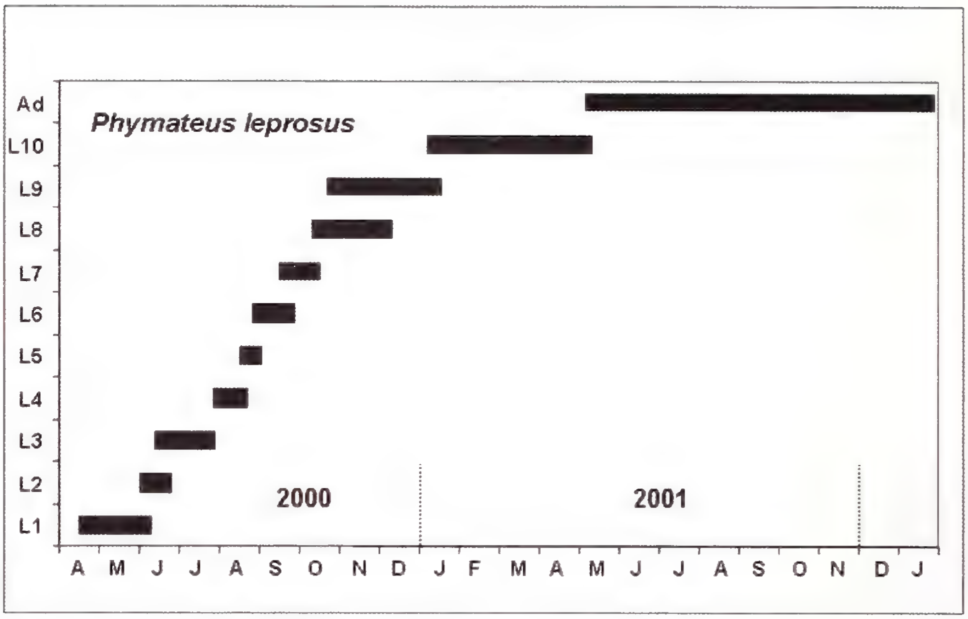

Fig. 4. Biennial life cycle of laboratory-reared *Phymateus leprosus*, starting with hatchlings, collected in late April in the Eastern Great Karoo (S.A.) and brought to the laboratory at Jena University.

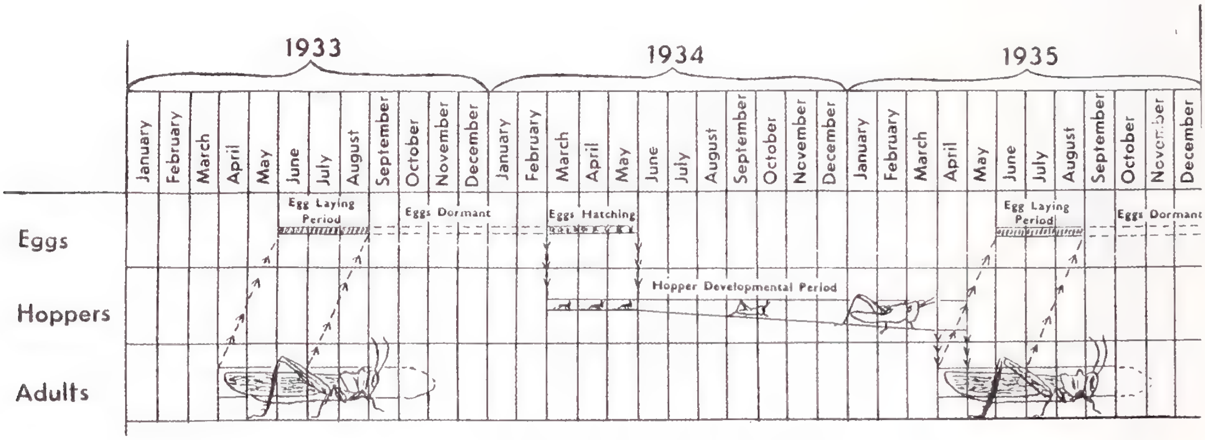
1933
1934
1935
January
February
March
April
May
June
July
August
September
October
November
December
Eggs
Hoppers
Adults
Egg Laying Period
Eggs Dormant
Eggs Hatching
Hopper Developmental Period

Fig. 5. Biennial life cycle of *Phymateus leprosus* in the field in the Eastern Cape Province, South Africa (detail from BISHOP 1940).

slightly within an instar (exuviae). According to our observations, the two prominent tubercles on the pronotum separating *P. leprosus* from other *Phymateus* species are distinctly visible from the 9th instar.

There is a major change in colouration after adult moult to a mainly green or red morph, briefly described in KÖHLER et al. (1999). In the green morph the head, pronotum, tegmina and legs are olive-green or greyish-green, whereas in the red morph these parts are dark red (except some individuals with a green pronotum). As far as we know, the red morph of *P. leprosus* seems to occur mainly in the Southern Great Karoo, whereas the green morph is distributed from the Eastern Cape (and the coast) to Transvaal.

The juvenile development extended over one year from 24. April 2000 (hatchlings collected in the field) to the beginning of May 2001 (adult moult in the laboratory) (Fig. 4). Despite the sunny place in the window and warm temperatures caused by a radiator (15–25 °C) development of the instars 8 to 10 retarded somewhat in the European winter months (Fig. 4). The duration of the instars varied from 4–6 weeks in instar 1–2 (May–June), 2–3 weeks in

Table 2. Reproduction parameters in *Phymateus species*. Mean (min–max).

Species	Origin	Ovarioles	Eggs in a female	Eggs per pod	Source
P. leprosus	S. Africa		340, 367		Bishop (1940)
	S. Africa	360, 480			Köhler et al. (1999)
	S. Africa	116, >187	157		present ms
P. viridipes	Eritrea		287 (233–335) [n=12]	135 (108–151) [n=6]	De Lotto (1951)
	Ghana			282	Chapman (1962)
	Kenia	200±10 [n=?15]		162 (60–231) [n=?15]	Kaufmann (2000)
	Malawi	>146			present ms
Phymateus sp.		393			Uvarov (1966; cit. Phipps)

instar 4–7 (July–September), 4–6 weeks again in instar 8–9 (October to January) and finally about eight weeks in instar ten (February–April). This phenology nearly perfectly fits with field observations over five years (1933–37) in the Eastern Cape Province by Bishop (1940) and with observations of adults in the Karoo (Köhler et al. 2001b) (Figs 4 and 5).

3.3. Adult development

One male and four females survived to adult moult, but one female died during the adult moult. After final moult, two females developed with somewhat scrambled tegmina and alae, only the male and one female had more or less normally folded wings. The adults eclosed in early

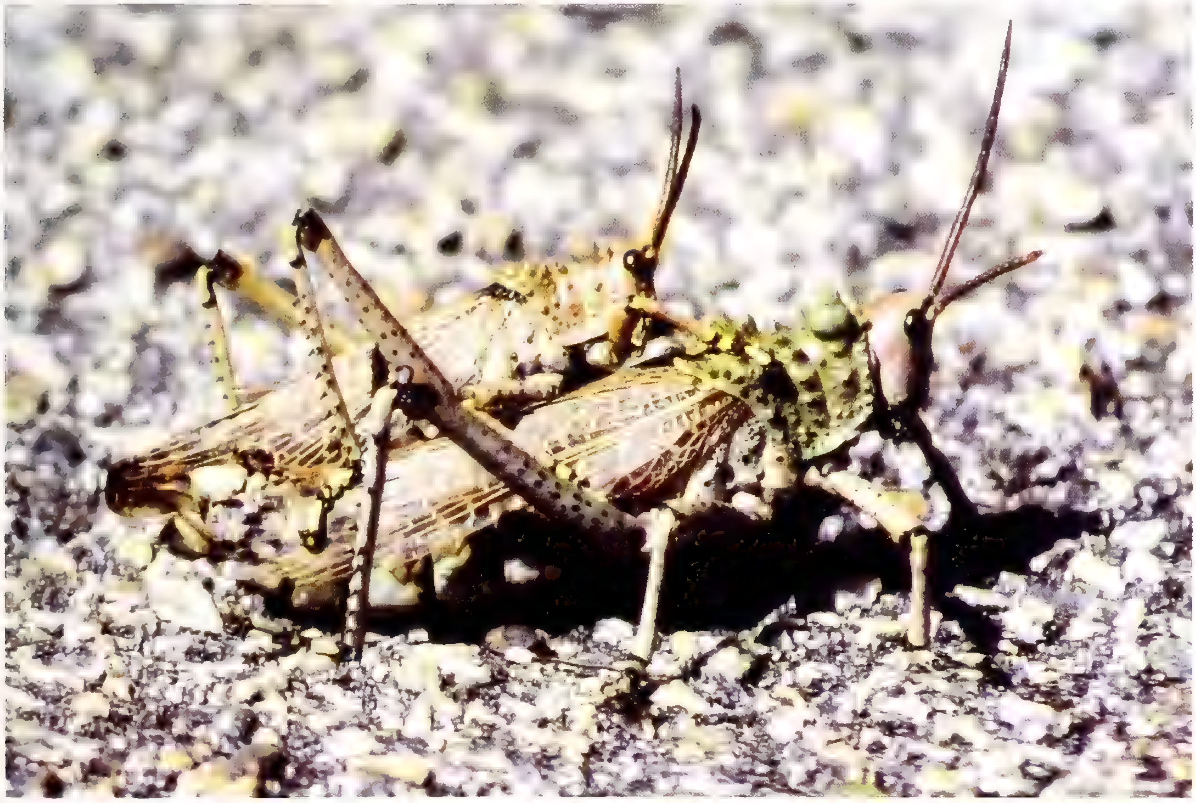

Fig. 6. Mating *Phymateus leprosus* in the field. Blyde River Canyon, N-Transvaal, South Africa, January 1995. Photo: K. Reinhardt.

May 2001, the last female died on 28. January 2002, resulting in a maximum adult lifespan of about eight months (Fig. 4). Two other females died on 9. July and 31. August 2001, reaching only two resp. four months of lifespan, which was not related to wing folding failure. The adults obtained were all of the green morph and in the four body parameters measured (length, pronotum, postfemur, forewing) smaller than individuals from the wild in the Southern Karoo near Prince Albert (P.A., Köhler et al. 1999). The only reared male reached about 50 mm body length (P.A. 53–62 mm) and 30 mm postfemur length (P.A. 27–34 mm), and the three reared females reached body lengths of 58–62 mm (P. A. 67–83 mm) and postfemur lengths of 30–33 (P.A. 32–40 mm).

Between 6. August and 10. September 2001 on six days it was observed that the male settled on the back of the female with the normal developed wings, although without actual coupling of the genitalia. This behaviour was seen mostly in the morning between 8:45 and 9:30 hours, on one occasion extending to 14:00 hours, and one case was seen only around 15:00 hours (Fig. 6).

On 3. August 2001 a plastic cup with a mixture of garden soil and fine sand was put into the terrarium, but no egg pod found on 11. December 2001. During these months no egg-depositing behaviour was observed nor were egg pods found on another medium.

The dead female from 9. July 2001 was in a reproductive stage (III) with 116 fully developed terminal oocytes (6.0 mm long, 1.5 mm in diameter). The female, which died on 31. August 2001, was around the ovulation (IV) and had 157 light brown eggs. The third and oldest female, which died on 28. January 2002, was in the pre-reproduction stage (II) and had still poorly developed ovarioles with more than 100 on the left and more than 87 on the right (not clearly separated). Similarly, a female *P. viridipes* collected on 14. September 2001 (Mulanje Mountains, Malawi, K.R.), also had very thin, undeveloped ovarioles (stage II) with at least 75 and 71 on either side. Summarizing the few available exact reproduction data from the genus, a broad variability has been detected reaching in reared *P. leprosus* from 116 to >187 ovarioles resp. eggs per pod and in wild females from 340–480. In *P. viridipes* these numbers vary mainly between 100 and 300 (Tab. 2).

4. DISCUSSION

Because of their occasional economic importance, the distribution and biology of the ten *Phymateus* species are summarized in the "Locust and Grasshopper Agricultural Manual" (Anonymous 1982). In addition to its considerable body size, members of the genus *Phymateus* exhibit at least five common characteristics: polyphagous on trees and shrubs, hopper aggregation behaviour, slow juvenile development, late adult maturation, and complex defence strategy of the adults. In *P. leprosus*, four of these characteristics are treated in the present paper, whereas the complex defence behaviour of this species was described as early as 1940 in Bishop (1940) and recently in Köhler et al. (1999), but it is well-known in *Phymateus* species in general (De Villiers 1985, Whitman 1990).

4.1. Food plants and rearing

The biology of *P. leprosus* has been studied only once nearly 70 years ago by Bishop (1940) in the Eastern Cape Province, South Africa, where this species became very abundant in 1933 near Coega, Port Elizabeth district. It invaded farmlands, causing considerable damage by feeding on pumpkins and other crops, and in a citrus nursery. In general, pyrgomorphid grasshoppers are non-graminivorous (Gandar 1982). However, all *Phymateus* species use a wide range of food plants, including toxic families like Euphorbiaceae, Asclepiadaceae, and Apocynaceae, as well as many crop species and garden plants with preferences for trees and shrubs (Anonymous 1982, Sithole 1986). In the milkweed (genus *Asclepias*) the cardiac glycosides proved to be phagostimulants in *P. leprosus* (Seibt et al. 2000).

Despite this, there are few rearing attempts and therefore the juvenile and adult development is rarely documented, possibly because of the high early mortality and because it is time-consuming to follow the very extended life cycle. There are two studies in *P. viridipes* (De Lotto 1951, Kaufmann 2000), one in *P. morbillosus* (Reyneke 1941) and one in *P. leprosus* (Bishop 1940) that report successful rearing of laboratory populations over their complete life cycle. For *P. leprosus* Bishop (1940) used mass and single rearing, but failed to ascertain the exact number of and the differences between the instars due to continuous high hopper mortality. Our hoppers suffered from a very high initial mortality, possibly caused by the unusual food plants, despite them being from the same families, Asclepiadaceae and Euphorbiaceae, as those eaten in the field (Bishop 1940, Köhler et al. 1999). Finally, our rearing showed that after a period of habituation a complete development of the leprous grasshopper up to the adult stage is also possible with non-native food plants. As secondary plant compounds, *Vincetoxicum arundinaria* contains bitter glycosides, whereas in the milk of *Euphorbia cyparissias* some phenolic substances were found (Hegnauer 1962–2001). Our successful rearing with *Rubus* spec. as food plant from instar 8 to the death of adults suggests that leaves of *Rubus* alone are sufficient for *Phymateus* in captivity.

4.2. Hopper aggregation

Several species of Pyrgomorphidae (and of Romaleinae) are typically gregarious as hoppers, but not as adults, a phenomenon named as juvenile gregariousness by Uvarov (1977). In the *Phymateus* species hitherto studied at most the young hopper stages remain gregarious forming dense aggregations on the food plants and bands of at least hundred individuals moving on the ground (e.g. *P. morbillosus* – Reyneke 1941, *P. aegrotus* – Kevan 1949, *P. viridipes* – De Lotto 1951, Chapman 1962). In later instars the tendency to aggregate becomes weaker (Uvarov 1977), and immature adults tend to disperse, but reaggregate to some extent for mating and oviposition (Roffey 1964, Rowell 1967). In *P. leprosus* this aggregation behaviour, as here observed for a bulk of first instar hoppers, was already described by Bishop (1940) occurring immediately after hatching in the field and also in captivity. He observed that after any disturbance (even the shadow of the observer) the hoppers scattered in all directions in search of dense vegetation, and later they reaggregated again. This suggests that dispersion rather than aggregation is an anti-predator behaviour. In the same manner the hoppers behaved when collected in the field and brought into a plastic contain (S.R.). According to observations of De Lotto (1951) on *P. viridipes* and the few observations presented here on *P. leprosus*, aggregation is also affected by the circadian light-dark-regime. This suggests that hopper aggregation seems to have a thermoregulatory function.

4.3. Instar number and phenology

Apparently, the hoppers of all *Phymateus* species are very similar in colouration and morphological details and hard to distinguish, something that already Karny (1910) had to confess. So Bishop (1940) described juvenile stages of *P. leprosus*, which resemble considerably those of *P. viridipes* from Eritrea, described in detail and with fine drawings by De Lotto (1951).

In *P. leprosus* Bishop (1940) estimated from mass rearing at least six juvenile instars in both sexes. In *P. viridipes* seven instars (De Lotto 1951), or six (males) and seven instars (females) were exactly observed (Kaufmann 2000). Differing from both studies, we found altogether ten instars in males and females, which is the highest number presently known in the Acridoidea. Previous maxima reached up to seven to eight also in the Pyrgomorphidae, and nine instars in both sexes of one species, the Bombay locust, *Patanga succincta* (Ramsay 1964, Uvarov 1966). The instar number in Caelifera is relatively stable (despite unfavourable rearing conditions), so in several acridoid species variability by one instar has been shown with geographic origin or food quality (Ramsay 1964, Uvarov 1966), but never three or four additional instars as observed here.

Because of their long juvenile and adult development *Phymateus* species have a biennial life cycle with reproducing adults occurring every two years. The onset of the cycle may vary geographically (Uvarov 1977, Anonymous 1982). According to Bishop (1940), *P. leprosus* from the same region as our individuals, occurs in the wild from June to March as eggs in the soil with a dormancy period of at most six months (September to February). From March to next March the hoppers and nymphs develop, and from March to November the adults are present. Because of an extended egg-laying period over three months a considerable overlap of all stages from two to three months occurs in the field (compare Fig. 5). Such long duration of juvenile and adult period in the field corresponds closely to our rearing results, although the cycle is slightly delayed compared to that presented by Bishop (1940). When the hoppers were brought to Central Europe, the altered temperature and photoperiod may have had some influence on the developmental period. This is apparent both in the variable duration of the instars and in the development of the adults. Our first adults moulted in May, whereas Bishop (1940) mentioned April, and in 1995 a Karoo population of immature adults occurred even in mid-March with still poorly developed ovaries in the females (Köhler et al. 1999, 2001b). The ovarian maturation should last about two months, so we found in captivity females with fully developed eggs in July/August, but not in January. Apparently, no egg pod of *P. leprosus* has, as yet, been found in the field. In addition, females in captivity never laid eggs, despite a large number of reared adults (Bishop 1940) and a few observed mating attempts in our culture. So the information about egg numbers was reached by dissecting gravid females (Bishop 1940, Köhler et al. 1999). The few known reproduction parameters in the genus *Phymateus* show for *P. leprosus* and *P. viridipes* a considerable variation in ovariole number, eggs in a female and eggs per pod (Table 2). This can be explained by a broad local and yearly variation of climate, influencing the population dynamics and food plant availability of the biennial bush grasshoppers.

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The Impact of Body Mass on Morphological Integration in Avian Skeletons (Aves, Fringillidae; Carduelinae, Fringillinae)

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Abstract. The dependence of the individual and of correlated skeletal variables of Carduelinae and Fringillinae upon body mass (=size) was tested by means of multiple regression and single linkage R-cluster analyses. The most obvious result is the significantly high degree of body mass dependences of all individual variables within the three functional complexes feeding, hind limb locomotion and flying. Elimination of body mass as a measure of size decoupled several units of correlated variables. Nevertheless the general robustness of units was strong but the removal of "size" had an impact on the extent of morphological integration, measurable as agglomeration level of variable units. Body mass (size) in our sample thus influenced the quantity rather than the quality of morphological integration. The key feature in fringilline/cardueline skeletal morphology – coevolution of skull and hind limb traits – thus appears to be relatively unconstrained by size.

Keywords. Size, ecomorphology, functional complexes, biological roles, skeletal morphology, developmental genetics.

1. INTRODUCTION

1.1. The role of body size in avian morphology

Body size has been identified as an important factor driving the diversification and evolution of organisms. OLSON & MILLER (1958, 1999), e. g. quantified size as a strong integrative force of morphology, FAIRBAIRN (1997) identified its role in sexual dimorphism, KLINGENBERG & SPENCE (1997) analyzed its function in life-history evolution. BONNER (2004) proposed a third size dependent rule besides the already well known "weight-strength-rule" and "weight-surface-area-rule". His "weight-complexity-rule" explains that increase and decrease in size of organisms are strongly related to increase and decrease in complexity in general, from differentiation of cell types to the social organization of organisms.

These examples implement size as a morphological key feature in the organization of life, at all hierarchical levels from the individual to species (BARBOSA et al. 2000; BONNER 2004; CHERNOFF & MAGWENE 1999; PETERS 1993).

Size, as the physical magnitude of objects, can be quantified using either measures or weights. Linear length measures are used to seize both the two dimensional area as well as the three dimensional volume, whereas weight quantifies the proportionality to volume alone. Measures widely accepted to represent overall size of organisms include also factors like the first principal component (BOOKSTEIN *et al.* 1985; ZELDITCH & FINK 1995; LEISLER & WINKLER 2006), landmarks or ratios. BJÖRKLUND & MERILÄ (1993), e.g. used orthogonal rotation to remove size from species mean vectors, LEISLER (1980) calculated the cube root of a compound measurement of the body core skeleton (sternum length plus pelvis length plus coracoid length) times (sternum width plus pelvis width) times height of crista sterni as measure for "body size", following HOERSCHELMANN (1966).

For the characterization of volume, body mass is the adequate measure. Several rules explaining the constructional constraints on morphology are related to body mass: The "weight-strength-rule" already mentioned above, explains why e.g. longer arms, wings and legs have to be proportionally thicker than shorter ones, the "weight-surface-area-rule" describes physiological relations of e.g. gas diffusion in large versus small lung surfaces. These are geometric growth laws, that explain the change of proportions – so-called allometric relations – within a biological organism. The underlying process is differential growth during development brought about by differences in the growth rates of the various parts (WADDINGTON 1966).

In small bodied flying vertebrates, flight imposes identical physical constraints on the flying organism that lead to a functional symmetry in body sizes (MAURER et al., 2004). The body plan of birds is primarily constrained by the weight-strength-rule, that regulates flying ability. In extant species 22 kg is the limit for take off; the worldwide tiniest bird is the Bee Hummingbird, *Mellisuga helenae,* found in Cuba and weighing from 1,6–1,9 g (CHAI 1999). The most successful clade in modern birds, the passerines (or perching birds, Passeriformes) have miniaturized to an average body mass minimum of 4,5 g in some tropical species (Black-faced Flycatcher Warbler, *Abroscopus schisticeps,* Broad-billed Flycatcher Warbler, *Tickellia hodgsoni,* Cuban Gnatcatcher, *Polioptila lembeyei*; DUNNING 1993). The heaviest and thus largest song bird, the Raven, *Corvus corax,* from Alaska weighs 1.240 g. Perching birds successfully evolved and radiated within any terrestrial habitat –with exception of the polar regions where their occurrence is physiologically constrained by the weight-surface-area-rule.

1.2. Key features of the carduelid skeleton

Our paper focuses on the impact of body mass on the architecture of the avian skeleton, taking the song bird subfamilies Fringillinae and Carduelinae as a case study. Morphological diversity in skeletal elements in this phylogenetic entity (clade, monophylum) is mostly confined to changes in overall size (BJÖRKLUND 1991, 1994; VAN DEN ELZEN & NEMESCHKAL 1986, 2006; NEMESCHKAL & VAN DEN ELZEN 1990, VAN DEN ELZEN & NEMESCHKAL 2006). Differentiations in shape are (despite their unquestioned ecological importance) only expressed as an insignificant portion of the total variation. Whereas three shape axes explained only 9,3 % of variance, the size axis accounted for 85,5 % of variance (VAN DEN ELZEN & NEMESCHKAL 2006). The observed pattern has been identified as a general rule in passerine birds by BJÖRKLUND (1994, 2006). "….making species to be larger or smaller copies of each other, all moving up and down a common line of allometry". Mapping of skeletal variables along the first principal components (NEMESCHKAL & VAN DEN ELZEN 1990) revealed, that morphological diversification in Fringillinae and Carduelinae focuses on variables of the beak. Thus, morphological change in these subfamilies is mainly reflected in feeding mechanisms.

In terms of ecomorphology, a discipline taking the biological role of morphological structures under consideration (BOCK & VON WAHLERT 1965), elements of the avian skeleton belong to three different functional complexes: skeletal elements of the skull and beak are allied to the feeding complex, wing bones, pectoral elements and bones of the shoulder girdle represent the flying apparatus and skeletal elements of pelvis and legs the hindlimb locomotion complex. In the carduelid skeleton, nevertheless, units of covarying variables (UCCs) contain combinations other than proposed by the functional complexes described above. These UCCs were detected to reflect units carrying out common biological roles. Besides a more or less undisturbed module of the "flying complex", formed solely by wing bones plus elements of the shoulder girdle, the variables of the feeding and hindlimb locomotion complexes were united in one single common cluster, and demonstrate the superimposure of feeding on hindlimb locomotion.

In search of additional modern approaches in the study of morphological integration, CHERNOFF & MAGWENE (1999) propose a hierarchical framework for integrative hypotheses: Morphological variables are judged as integrated at the broadest, i. e. the uppermost inclusive level due to their covariation with size. At a less inclusive level variables covary due to developmental and/or functional associations and at still lower levels due to anatomical (spatial) associations. Starting out from physics we may assume that changes of singular parts from a macroscopical physical (e. g., mechanical) system will be ruled by various law-dependencies when the whole system changes size (e.g., mass). As a consequence, we test in the current study the dependence of individual and correlated skeletal variables upon body mass taken as a measure of size.

1.3. Presumptions

Based upon our knowledge from preceding analyses (VAN DEN ELZEN, NEMESCHKAL & CLASSEN 1987, NEMESCHKAL & VAN DEN ELZEN 1990, NEMESCHKAL, VAN DEN ELZEN & BRIESCHKE 1992, VAN DEN ELZEN & NEMESCHKAL 2006) our hypotheses are that:

1. a significant dependence of skeletal variables on body mass exists. It is expected to differ between variables and to be highest in beak elements;
2. thus the three theoretical functional complexes -feeding, hindlimb locomotion, flying- differ in their size dependence;
    a. variables of the feeding apparatus – showing highest morphological differentiation between species – should exhibit the largest amount of size dependence,
    b. elements of the hindlimb locomotion complex and of the flying apparatus are thought to show lesser dependence, as of lesser interspecific variability.
3. units of variables (UCCs) are also expected to be size dependent, elimination of "size" is thought to decouple variables within units; decoupling is expected to occur particularly within "mixed" variable units of beak and hindlimb osteometrics.

2. MATERIAL AND METHODS

In 313 specimens, representing 43 species (Table 1), 42 equivalent skeletal variables (measurements of bone lengths, widths and depths) were taken, as described in detail in NEMESCHKAL (1999). Twenty measurements stem from the feeding apparatus, 13 represent the flying apparatus and 9 hindlimb locomotion (Table 2).

Firstly, centroids of 43 species over 42 variables were built from the log scaled original data matrix consisting of 313 specimens. This procedure was essential, because body mass data were available as species means only. Morphological variation between species was then quantified by the total variance of species centroids. Body mass variation in the actual fringilline-cardueline sample ranges from a maximum of 54 g in the Hawfinch *Coccothraustes coccothraustes* to a minimum of 9 g in neotropical siskins (Table 1). To test hypotheses about size impact, linear regression analysis was applied. Log transformed species means of body mass were taken as predictor variable and each of the 42 skeletal measurements as criterion variable. The 42 resulting residuals are used as the variables under study – the variables corrected for body mass (= variables of which size was partialized out; BCM). The coefficients of determination between body mass and original variables (Table 2) were tested for significance using random bootstrap (1000 replicates each; for computer programme package see NEMESCHKAL (1999)). They are figured as profiles of variance (Figs 1, 2). Single linkage R-cluster analyses were chosen to figure correlations of original data (Figure 3- BO; based upon the variable intercorrelation matrix between species means for original data) and correlations data corrected for body mass (Fig. 3- BCM; variable intercorrelation matrix between species means for body mass adjusted data). Units of correlated variables were taken into account, when they agglomerated at the uppermost quartile ($r^2 > 0.924$) in the original dataset **and** reappeared in the size corrected dataset again. E-units are stable clusters with topological identity of variable positions in both the R-cluster analyses of original data and the body mass corrected data set. S-units are less stable units built of identical variables but with topological differences between analyses of original and size corrected variables.

3. RESULTS

The most obvious findings are on the one hand the significantly high degree of body mass correlation of all individual variables (Fig. 1) and on the other hand the robustness of several covarying variable units found in both the original and the "residual" data set, adjusted for body mass (Fig. 2).

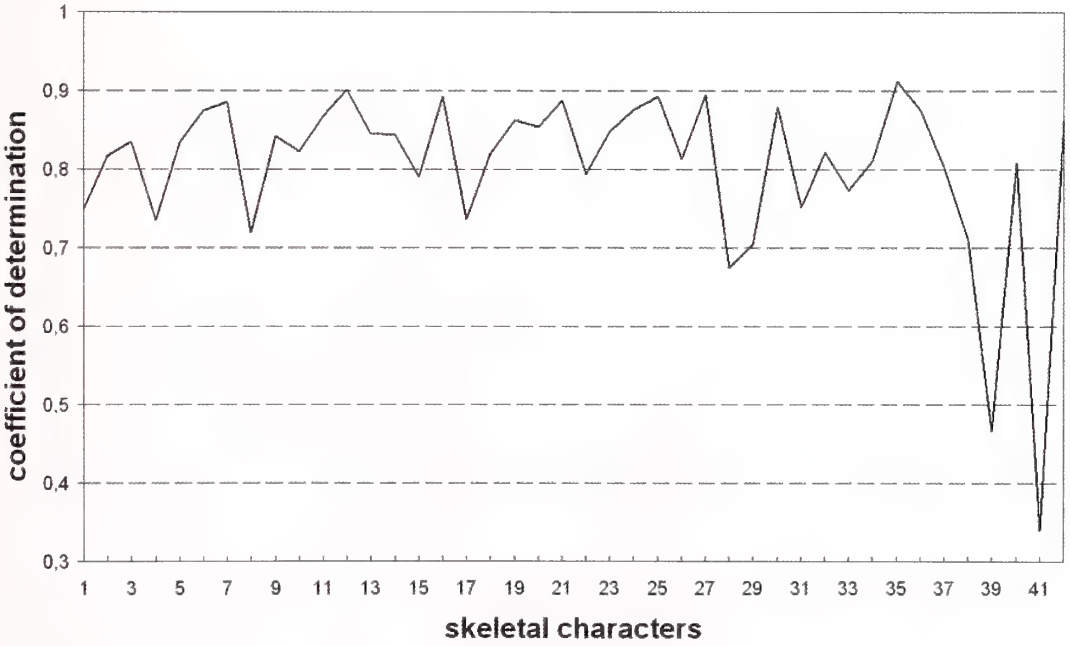


Fig. 1. Dependence of 42 skeletal characters on body mass as shown by coefficients of determination.

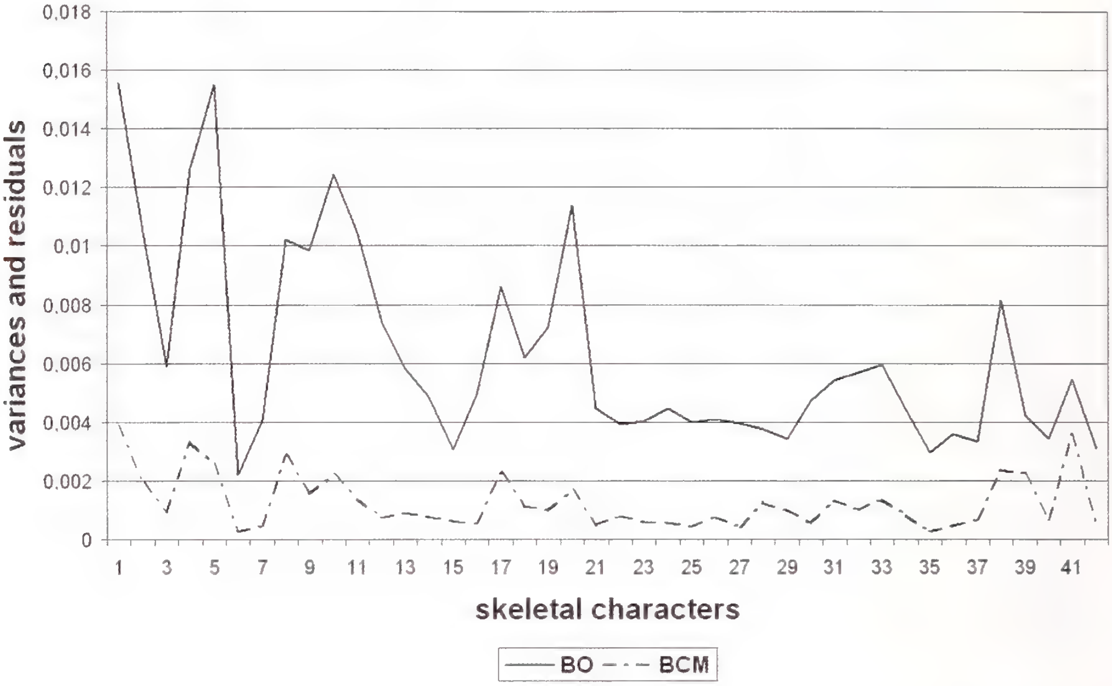
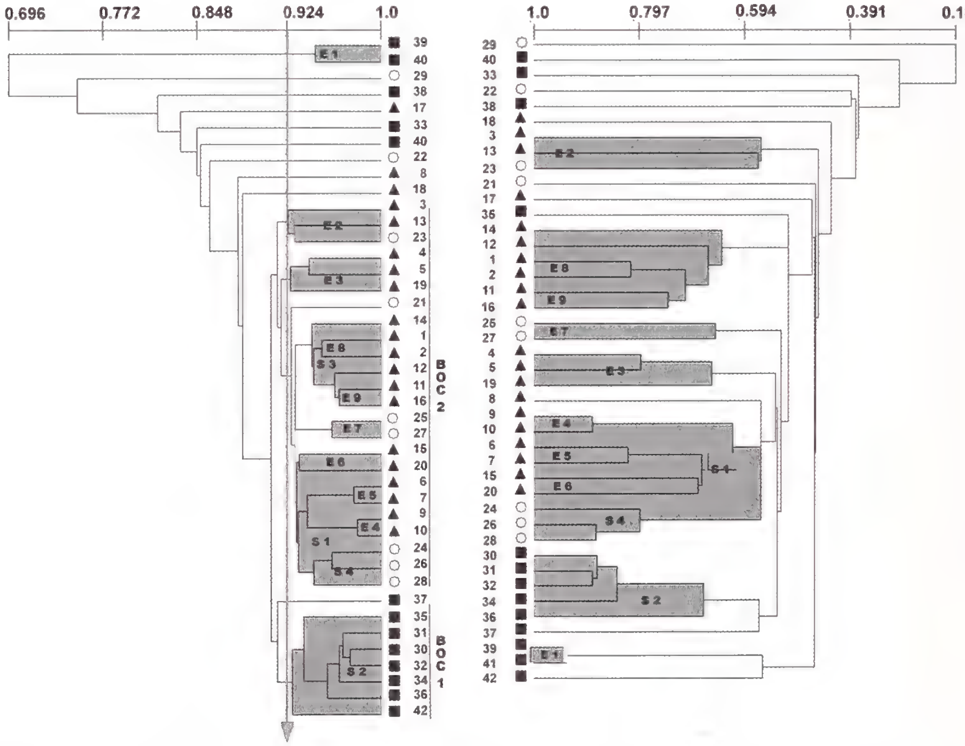


Fig. 2. Comparison of variance profiles. Variance of original characters (BO) occur in the upper line and residuals for characters corrected for body mass (BCM) at the bottom.


0.696
0.772
0.848
0.924
1.0
E 1
E 2
E 3
E 8
S 3
E 9
E 7
E 6
E 5
E 4
S 1
S 4
S 2
39
40
29
38
17
33
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22
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16
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27
15
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7
9
10
24
26
28
37
35
31
30
32
34
36
42
BOC 2
BOC 1
1.0
0.797
0.594
0.391
0.188
29
40
33
22
38
18
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E 2
E 8
E 9
E 7
E 3
E 4
E 5
S 1
E 6
S 4
S 2
E 1

Figs 3. Single linkage R-cluster analysis of original data (BO; left) and of body mass corrected data (BCM; right). Black squares indicate measures of the pectoral girdle and forelimbs, black triangles mark skull measurements and open circles measures of the pelvic girdle and hindlimbs. Clusters are explained in the text.

3.1. Influence of body mass on individual variables

All 42 variables are correlated with body mass at a high significance level ($p< 0.001$) as revealed by random bootstrap procedures. The degree of correlation with "size", measured by coefficients of determination (COD) between (log transformed) original data of species means and body mass, is highest in coracoid length (variable number 35; COD=0,91), post orbital length (12; 0,90) and equal at COD= 0,89 in tibiotarsus width (27), total skull length (16) and synsacrum length (21). The largest amount of body mass independence exhibit carpometacarpus (41) and ulna lengths (39; COD= 0,34 and 0,47) as well as tarsometatarsus length (No 28) and width (29; COD= 0,70, resp. 0,67) and proximal end width of the humerus (38; COD= 0,71). Skull variables in general reveal the highest correlation with body mass, hindlimb and forelimb variables indicate a larger variation in their correlation with body mass.

A comparison of variance profiles of original and size corrected skeletal variables (Fig. 2) confirms and strengthens these findings: The relatively higher variances in the original variables appear smoothened in the size corrected residuals (BCM; bottom line in fig. 2), indicating that the largest amount of total variance between species is due to a "size factor", measurable by body mass. This especially holds true for skull variables (skeletal variables 1–20) and less for hindlimb and forelimb measures (skeletal variables 24–29, 37–42).

3.2. Influence of body mass on united variables

The single linkage cluster analysis of original data (Fig. 3) extracted two main units fused at a high level, several disintegrated variables and one isolated variable set (E1). The module BOC 1 is composed of the variables of the flying apparatus, mainly its "engine-supporting" part, including measures of sternum, coracoid and scapula. Wing measures that represent "flight performance" are highly disintegrated, only humerus length (37) and carpometacarpus width (42) are included. The second main module BOC 2 combines skull and hindlimb measures.

The two main modules BOC 1 and BOC 2 are composed of two different types of subsets: Robustness is observed in nine smaller units (E1–E9), where only two to three variables are coupled. Similar structure is maintained after correction for size in four units (S1–S4), including three to 17 variables as well as including several of the stable units (E4–E9). Whereas, for example, femur length (24) and tibiotarsus length (26) are next neighbours in the S4 cluster in BO, in BCM tibiotarus length (26) and tarsometatarsus length (28) are agglomerated at the highest level. The larger S1 and S2 units also include some of the smaller, topologically stable E units: E4–E6 always occur within S1, E8–E9 within S3, S4 is always part of S1.

BOCs identified in the R-cluster analysis of original data are to a great extent also found in the analysis of body mass corrected data (Fig. 3). Again in the body mass corrected data analysis, a main cluster composed of engine-supporting variables from the flight complex (S2 in BOC1, fig. 3) opposes a main cluster structured by a mixture of skeletal elements of the feeding and hind limb locomotion apparatus characters. The main differences to the original data analysis are the rather low agglomerative level (coefficients of determination in the "size-corrected" dataset being two to three times lower than in the original dataset), reduction of the involved variable units and some changes in variable topology. BOC2, that was composed of S1 (including S4), S3, E2, E3 and E7 in the original dataset, comprises in the size corrected data set only S1 (including S4) and E3, the remaining components – units S3, E2 and E7 – are clustered at lower agglomeration levels.

Subcluster S1 differs in its hierarchical structure of agglomeration levels of E units and arrangement of variables within S clusters. In S2 sternum length (30), keel length (32) and keel depth (31) are differently arranged, in S3 post orbital length (12), and within S4 femur-, tibiotarsus and tarsometatarsus lengths (24, 26, 28) changed their position along branches.

In both illustrations of single linkage R-cluster analyses (Fig. 3), E1 shows up as a more or less disintegrated unit. It consists of measures of ulna (39) and carpometacarpus lengths (41), which are tied together at a relatively high agglomeration level, especially in the analysis of "size-corrected" data, in which both measures are combined with carpometacarpus width (42).

4. DISCUSSION

4.1. Size and morphological integration

Do these results confirm or contradict our predictions and expectations of hypotheses on morphological integration? Corroborating our first assumption, a general body mass dependence was identified at a high significance level for all individual characters within all three classical functional complexes. "Size" could thus be confirmed as a strong integrative force in cardueline and fringilline skeletal morphology. Variability was, as assumed in our second hypothesis, relying to a greater extent on body mass in skull and beak measurements than in characters allied to the other functional complexes. Elimination of "size", decoupled,

Table 1. List of species under study, their body masses and information sources. Sources: DU= Dunning 1993; RE= labels of specimens at ZFMK, Bonn; RO= McLean 1988; WA= Ward 2003.

Species	**body mass in g**	**sources**
Fringilla montifringilla	24	DU
Fringilla coelebs	21,4	DU
Coccothraustes coccothraustes	54	DU
Pyrrhula pyrrhula	21,8	DU
Pinicola enucleator	56,4	DU
Loxia curvirostra	40,38	DU
Chloris chloris	27,8	DU
Chloris sinica	31,3	DU
Acanthis flammea	13	DU
Carduelis carduelis	15,6	DU
Linaria cannabina	15,3	DU
Agriospiza flavirostris	15,4	DU
Rhodospiza obsoleta	25,5	DU
Spinus spinus	14,5	DU
Spinus cucullatus	9	RE
Spinus barbatus	16,6	DU
Spinus xanthogaster	12,7	DU
Spinus yarrellii	9,5	RE
Spinus psaltria	9,5	DU
Serinus pusillus	11,6	DU
Serinus serinus	11,2	DU
Serinus syriacus	12,1	BE
Serinus canicollis	13,8	DU
Serinus citrinella	12	DU
Alario alario	11,8	RO
Serinus canaria	12,97	DU, RE
Ochrospiza reichenowi	11,5	RE
Ochrospiza atrogularis	11,4	DU
Ochrospiza leucopygia	9	RE
Ochrospiza mozambica	10,6	DU
Ochrospiza dorsostriata	14,4	DU
Ochrospiza xanthopygia	10	RE
Crithagra gularis	15,5	DU
Crithagra striolata	22,4	DU
Crithagra albogularis	25,9	DU
Crithagra donaldsoni buchanani	24	DU
Crithagra sulphurata	19,2	DU
Serinops flaviventris	16,3	DU
Crithagra mennelli	15,3	RO
Crithagra burtoni	29,9	DU
Dendrospiza hyposticta	15	DU
Dendrospiza scotops	15,4	RO
Pseudochloroptila totta	13,4	WA

as predicted in the third assumption, several units of correlated variables. Nevertheless, contradicting our expectations, displacement of variables from units or units from larger modules was low and robustness of units strong. Body mass (size) itself in our sample thus influenced the quantity rather than the quality of morphological integration and did not affect the key feature in fringilline/cardueline skeletal morphology – coevolution of skull and hindlimb variables.

According to classical hypotheses on morphological integration, "size" is the uppermost integrative level, at deeper agglomerative levels, traits covary due to developmental or functional associations and at still deeper levels due to spatial adjacency (CHERNOFF & MAGWENE 1999) respectively morphological neighborhood (ALPATOV & BOSCHKO-STEPANENKO 1928). Indeed, in our study, removal of the first hierarchical layer "size", mostly effected the degree of morphological integration, measurable as agglomeration level of character units. Structure and relation of character compositions however remained to a great extent constant and robust. For variable units at the body mass reduced level, three types of trait correlations are identifiable: S-modules are subunits agglomerated at higher integrative levels within BOC1 and BOC2, the original, not body mass reduced, modules. E-modules that are not composed of characters from immediate morphological neighborhood or partial overlap (E4, E5, E9) can be assigned to two categories: Classical functional units (E2, E3, E6 and E7) are with one exception (E7) fused at lower agglomerative levels (below 0.6 COD) than the units of biological roles E1 and E8 (above 0.8 COD). Our findings thus corroborate the integrative hypotheses quoted above, that anatomical association is a primary integrative level in morphology.

4.2. Interpretation of the observed character modules

EBLE (2005) classifies four different kinds of modules in morphology:

1. modules due to structural relations,
2. modules of pleiotropic genotype-phenotype mappings,
3. developmental units (gene expressions, domains of epigenetic dynamics, regions with localized allometric growth) and
4. functional units.

We would like to extend the definition of the last category by modules accomplishing common biological roles (NEMESCHKAL et al. 1992) and thus differentiate between

4.a. mechanical functioning (like kinetics) and
4.b. biological functioning (like morphological traits used in e. g. feeding).

Units E4 (postorbital width and internasal width, 9, 10), E5 (skull width and interorbital maximal width, 6, 7) and E9 (premaxilla length and total skull length, 11, 16) may be explained by their immediate morphological neighbourhood and /or partial overlap ("rule of neighbourhood", ALPATOV & BOSCHKO-STEPANENKO 1928; structural relations EBLE 2005). Most of the other results allow for mechanical functional explanations, few for explanations of their biological roles. E2 is composed of two skull characters (caudal length of the mandible and quadratojugal length, 3, 13) and a pelvis measure (synsacrum distal length, 23). Whereas the first two skull variables are functional counterparts and act in seed husking, their –also body mass independent- correlation with a synsacrum length measure comes unawares. E3 combines two mandible depths (4, 5) with quadratum length (19), characters functioning in the kinetism of the avian skull, especially in lateral bill movements enhancing seed husking (NUIJENS & ZWEERS 1997). Also units E6 (skull height and premaxilla depth, 15, 20) and E7 (femur and tibiotarsus width, 25, 27) are easier to explain by constructional constraints than biological roles. E6 depicts the interdependence of skull and beak height, E7 that of leg diameters, in E8.Only units E1 and E8 where measures of the flying apparatus (carpometacarpus (41) and ulna lengths (39)) respectively bill tip are tied together (length of pars symphysialis (1) with dentary length of the mandible (2)) allow for an interpretation of biological roles: The first unit comprises the feather-carrying bones of the wing, responsible for manoevrability in flight per se. Unit E8 represents "the bill tip grasp", a feeding tool well developed in carduelid finches (NEMESCHKAL et al. 1992).

S4 with the lengths of femur (24), tibiotarsus (26) and tarsometatarsus (28) obviously reflects a character pattern of concerting limb dimensions as guided by developmental processes during ontogeny (NEMESCHKAL 1999).

Comparison of interspecific correlation patterns (macroevolutionary pattern, this study Fig. 3) with infraspecific analyses of variable correlations (microevolutionary level, NEMESCHKAL & VAN DEN ELZEN 1994, fig. 7) reveal that six modules (E3, E4, E5, E7, E8 and E9 of this study) correspond to units also found within carduelid finches and three modules (E5, E7 and E9) even to units occurring within the phylogenetically distant pigeons. At the microevolutionary level NEMESCHKAL et al. (1992) provided evidence for clade specificity of variable units (modules) and their correspondence to expressions of developmental control genes (NEMESCHKAL 1999). Morphological modularity might generally be seen as product of developmental modularity, because morphological patterns of organization emerge in ontogeny (EBLE 2005). Consequently, each of the extracted variable complexes might additionally also correspond to developmental or body plan modules.

Table 2. Skeletal variables under study and their coefficients of determination. BO represent original data, BCM residuals for the body mass reduced variables.

Skeletal variables	Coeff. of determination
Skull measures	
01 mandible, pars symphysialis length	0,7014
02 mandible, dentary length	0,7641
03 mandible, pars caudalis length	0,7642
04 mandible, dentary depth	0,6924
05 mandible, pars caudalis depth	0,7883
06 skull width	0,8239
07 interorbital, maximal width	0,8353
08 interorbital, minimal width	0,6704
09 postorbital width	0,8048
10 internasal width	0,7856
11 premaxilla length	0,8240
12 postorbital length	0,86
13 quadratojugal length	0,7953
14 orbital width	0,7888
15 skull height	0,7280
16 skull length	0,8610
17 palatinum width	0,6176
18 pterygoid length	0,6932
19 processus orbitalis quadrati length	0,7988
20 premaxilla depth	0,7911
Pelvic girdle and hindlimbs	
21 synsacrum length	0,7748
22 synsacrum width	0,7076
23 synsacrum distal length	0,7464
24 femur length	0,8355
25 femur width	0,7781
26 tibiotarsus length	0,7675
27 tibiotarsus width	0,7562
28 tarsometatarsus length	0,6180
29 tarsometatarsus width	0,3034
Pectoral girdle and forelimbs	
30 sternum length	0,8413
31 keel depth	0,6897
32 keel length	0,7632
33 sternum, distal width	0,6617
34 sternum depth	0,7393
35 coracoid length	0,8401
36 scapula length	0,8114
37 humerus length	0,7644
38 humerus, proximal end width	0,6246
39 ulna length	0,3233
40 ulna width	0,6235
41 carpometacarpus length	0,2333
42 carpometacarpus width	0,6454

How genes and developmental pathways co-operate is best documented for the avian beak. It is constructed by multiple facial prominences (HELMS et al. 2005, HELMS & BRUGMANN 2007), where the frontal nasal mass (FNM), lateral nasal prominences (LNP), and maxillary prominences (MXP) comprise the upper beak and the mandibular prominence (MDP) forms the lower beak. The identities of facial prominences are specified early in the neural crest stage and may involve homeobox genes such as Hox (COULY et al. 1998) or MSX (BROWN et al. 1997, WU et al. 2006).

In metazoa, at least 17 signal transduction pathways operate to activate or repress different genes at distinct times and places in the embryo. Five predominate in early embryonic development: the Wnt, TGF-beta, Hedgehog, RTK, and Notch pathways. Five more are used in late development, and seven more in the functions of differentiated cells (GERHART 1999).

Diversity in beak shapes of Galapagos finches, e. g., is known to originate from the activity of a morphogenetic bone protein (BMP4 of the TGF-beta family; ABZHANOV et al. 2004) and calmodulin, a protein that binds and transports calcium ions (CaM; ABZHANOV et al. 2006). Whereas BMP4 stimulated growth of beaks along two dimensions, – it produced deeper and wider beaks and thus explained the linkage in the variation of these traits, – the authors found CaM as regulator of beak length. Thus in Galapagos finches, beak length develops independently from width and depth due to two different factors that lead to changes in growth along different dimensions (ABZHANOV et al. 2006). In ducks, chickens and cockatiels, BMP4 is also differently expressed (WU et al. 2004, WU et al. 2006). At late stages of development, chicken and duck embryos had two localized growth zones in the FNM, which melted in the chicken, but stayed separated in the duck. Ducks, moreover exhibited a wider FNM and more activity in another growth factor (fibroblast growth factor 8). In cockatiels a thicker FNM increased in a different direction and the mandibular prominence (MDP) was suppressed. BMP4 was involved in all species in mediating activity in all localized growth zones. Experimental overexpression in BMP4 altered beak shapes among all species and beak curvation was induced by asymmetric growth activity in a facial prominence. BMP4 was also found to be responsible for regulating a homeobox gene: As it increased the expression of MSX1, the authors suggested that MSX1 activity is regulated by the BMP pathway.

4.3. Conclusions

Under the assumption that BMP4 is a main regulator for the expression of developmental control genes in the avian skeleton, this protein, for instance, can be seen as a key growth factor accounting for size and shape variation in our skeletal variables. A developmental growth factor can also explain the strong size dependence of single variables, but cannot elucidate the interspecific correlation patterns of variable units. Thus in the light of current knowledge on gene expression variability and research in developmental genetics the classical view on morphological integration and genesis of modularity might be too onesided.

WAGNER et al. (2007) offer a broader approach to modularity. Summarizing empirical evidence, they discern between two levels: The elements the modules consist of and their kinds of interaction. Elements vary from molecular level (nucleotides) to morphological traits and their connections from physical to dynamical and statistical. They define three kinds of modules: Variational, functional and developmental modules, but stress a duality, as modules may belong to several categories at the same time. Units observed in the present study on cardueline/fringilline skeletal variables fall in the category of variational modules, as their measure is statistical. For the interpretation of variational modules the authors offer several answers: identical developmental origin, similarity of covariation and gene expression territories, and pleiotropic effects. So our variable units (or character complexes; NEMESCHKAL et al. 1992) can be defined not only as a duality but a plurality: according to their operability they are functional modules, according to their mode of exploration they are variational modules, and according to their genesis developmental modules.

The open problem is, whether modules arise through the action of natural selection or because of biased mutational mechanisms (WAGNER 2007). Both neutral models and models based on natural selection are offered: e. g. LYNCH (2007) favors the neutral model and stated that "... emergent biological features such as complexity, modularity, and evolvability, all of which are current targets of considerable speculation, may be nothing more than indirect by-products of processes operating at lower levels of organization." We do not follow the author in refusing natural selection and external evolutionary forces, but assume, that selection via fitness promotes certain phenotypes derived from their genetic basis and processes in ontogeny. Under the viewpoint of developmental constraints as internal evolutionary forces, we like to generalize the findings of WU et al. (2004, 2006) on the origin of beak shape in birds. The authors offer a more reconciling conclusion, that morphological diversity may be achieved by modulating prototypical molecular and cellular modules. Transforming growth factors may mediate the range, level, and duration of locally enhanced growth, thus providing a spectrum of morphological designs for selection (WU et al. 2006). Also Wagner et al. (2007) arrive at the conclusion that mutational processes (internal processes) favor the origin of modularity and selection pressures (external processes) reinforce the mutational bias.

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Occurrence of the Genus Microscolex (Oligochaeta, Acanthodrilidae) at Western Canary Islands

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Abstract. Two species of *Microscolex* are present in the western Canary Islands: *M. dubius* and *M. phosphoreus* (new record for Hierro*)*. The latter belongs to the modern fauna of the Canaries and was recently introduced by man. Both species prefer to live at the basal altitude level, mainly in the highly anthropized band between 50 and 300 m a.s.l. The habitat range of *M. phosphoreus* is rather narrow and its principal nucleus of dispersion are tropical fruit plantations (papaya, avocados and bananas); however, *M. dubius* is more diversified, its range is wide, even reaching into the native *Pinus canariensis* and laurel forests at the montane level. Other data provide evidence that the greatest number of specimens and locations are on the northeast slopes of the Canaries, as reflected in the first distribution maps of each of the islands. The biogeographical affinities with Macaronesia are discussed, along with the probable links with Latin America as a long-standing (500 year-old) source for importing agricultural and ornamental plants into the Canaries.

Keywords. Earthworms, Acanthodrilidae, Canaries, habitats, chorology.

1. INTRODUCTION

The taxonomy and distribution of the Acanthodrilidae have been under study for a long time, BEDDARD (1895) and MICHAELSEN (1900) having compiled comprehensive information on these annelids in their magnificent scientific works. They are well known in Australasia, the Neoarctic and Neotropical regions, where they are spread over a wide range of both anthropized deforested habitats and those with abundant vegetation (e.g. tropical forests). The family is increasing in numbers and distribution area, as revealed by successive biogeographical records and descriptions of new taxa (CSUZDI & SZLÁVECZ 2002; FRAGOSOS 1988; FRAGOSOS & REC FERNANDEZ 1994; REYNOLDS & RIGHI 1994; ZICSI & CSUZDI 1991).

In the Canary Islands, few acanthodrilids have been recorded in the literature to date. KRAEPELIN (1895) cites *Microscolex poulteni* (BEDDARD, 1892) as presumably from Tenerife but with no details. MICHAELSEN (1900) reports *Microscolex dubius* (Fletcher, 1887) and *Microscolex phosphoreus* (Dugès, 1837). Later, other authors merely copied them literally (COGNETTI DE MARTIIS 1906; BALDASSERONI 1912). More recent data were obtained during direct field surveys performed by BOUCHÉ (1973) and TALAVERA (1992a), in particular those concerning the presence of *M. dubius* in banana plantations and laurel forest in Tenerife. In any case, the taxonomy, ecology and chorology of the genus *Microscolex* Rosa, 1887 in the Canary Islands have been insufficiently studied. Therefore, in order to update and increase the data we have sampled a total of 22 districts and reviewed more than 1550 specimens, producing original iconography and the first species distribution maps for each island (Tenerife, La Palma, Gomera and Hierro).

2. MATERIAL AND METHODS

Specimens were collected mainly by qualitative sampling along routes of up to one Kilometre in length, so as to include a wide range of habitats with the greatest possible species diversity. A geologist's hammer was used for digging and specimens were picked out manually. Less frequently, 0.04 % formalin was poured over surface areas of 100 x 50 cm, providing complementary data on specimen abundance. The collected earthworms were usually transported to the laboratory inside plastic bags along with one Kilogramm of earth (winter time). After washing to remove the remaining earth they were submerged in 70 % alcohol, introduced into glass test-tubes containing 10 % formalin and left for four days, then finally conserved in 75 % alcohol. On very warm days and to avoid possible over-drying and desiccation, the worms were prepared and conserved "in situ" following the same steps.

In TALAVERA (1990a) keys were used to identify species. To prepare the original iconography the specimens were placed on a sheet of cork at the bottom of a beaker half-full of 70 % alcohol and the dissection was carried out under a binocular lens using an unsheathed razor blade and entomological pins. The specimens examined came from my own collections made during the Doctoral Thesis (1980–1986), and from surveys carried out personally between 2000–2004, as part of research projects financed by the General Directorate of Universities of the Canary Government. A minimum of five station were sampled from each municipal district and montane localities (total 35), distributed as follows: 14 in Tenerife, ten La Palma, four Gomera and seven Hierro.

These districts prospected (Fig. 1) are as follows: **1** Santa Cruz de Tenerife, **2** La Laguna, **3** Anaga, **4** El Rosario (Monte La Esperanza), **5** Acentejo, **6** Icod, **7** Daute, **8** Los

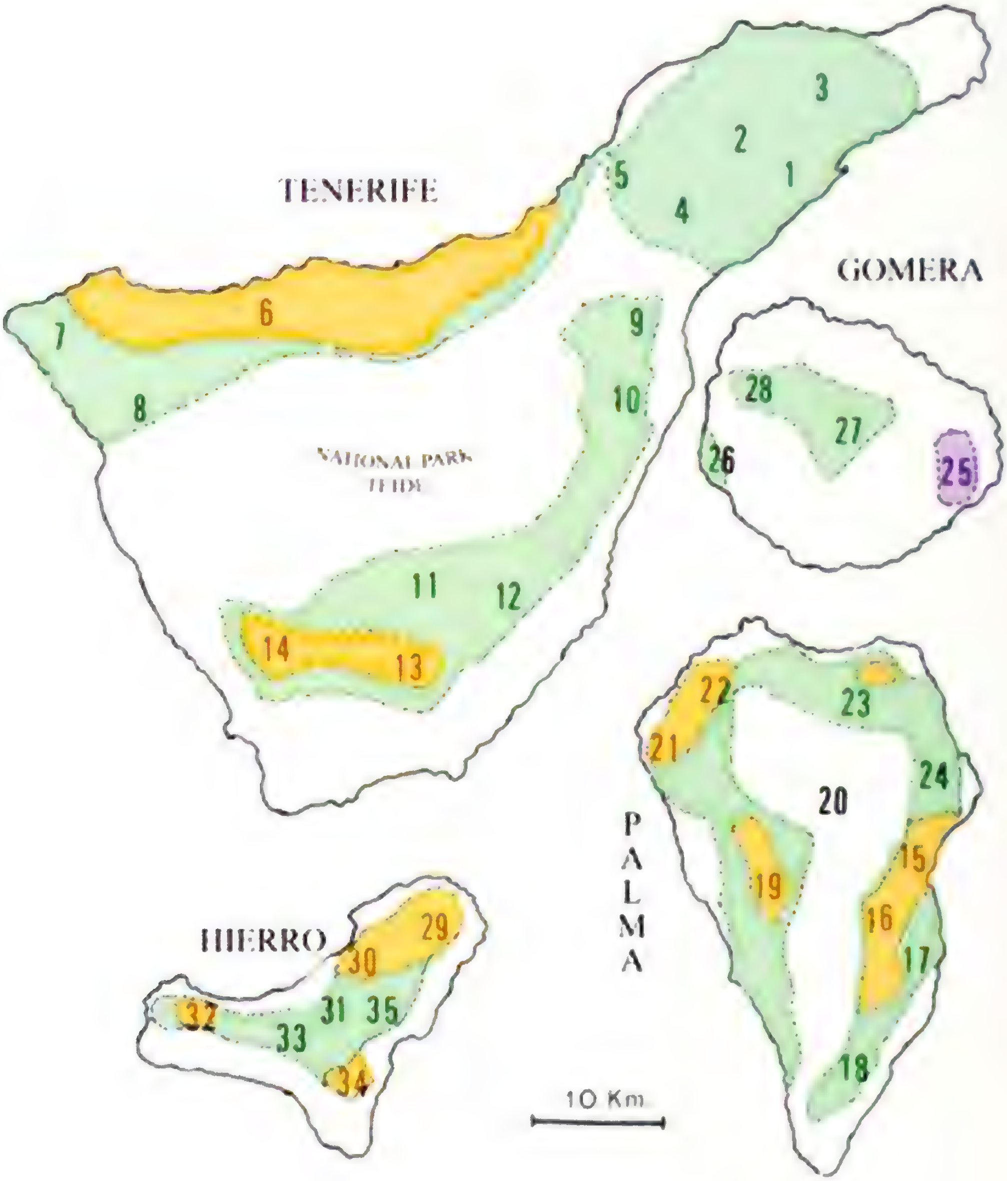

Fig. 1. Maps western Canary Islands showing of municipal district. Green, distribution of *Microcolex dubius*; Mallow, distribution of *Microscolex phosphoreus*; Orange, distribution of together species.

Silos, **9** Candelaria, **10** Güimar, **11** Chasna, **12** Abona, **13** Arona **14** Adeje, **15** Santa Cruz de La Palma, **16** Las Breñas, **17** Mazo, **18** Fuencaliente, **19** Valle de Aridane, **20** Taburiente, **21** Puntagorda, **22** Garafía (Cueva del Agua), **23** Barlovento (Las Cancelitas), **24** Puntallana, **25** San Sebastián, **26** Valle Gran Rey, **27** Hermigua (Cedro-Garajonay **28** Vallehermoso (Chorros de Epina), **29** Valverde, **30** Meseta de Nizdafe, **31** Frontera, **32** Dehesa **33** Julán, **34** El Pinar, **35** Tajace.

3. RESULTS

1550 earthworms assignable to *Microscolex dubius* and *Microscolex phosphoreus* were studied. Figs 1–3 show the main anatomical-morphological characters and the present range of distribution for each species.

Microscolex dubius (Fletcher, 1887)
Eudrilus dubius Fletcher, 1887
Microscolex dubius Rosa, 1890

Remarks. The morphological variability between the examined specimens is minor, except in the pigmentation (different tones of pinkish grey), and body length varying between 30–75 cm. Male pore and prostates tubular on 17. Genital papillae and spermathecae are generally absent, whereas small aracemose seminal vesicles nearly always appear in segments 11–12. A hydrophilic species tolerating high Na concentrations, it was found at humid sites rich in natural or artificial organic matter, and occasionally in soils with as little as 15.5 % relative humidity and 1.1 % organic matter (Buenavista, Tenerife).

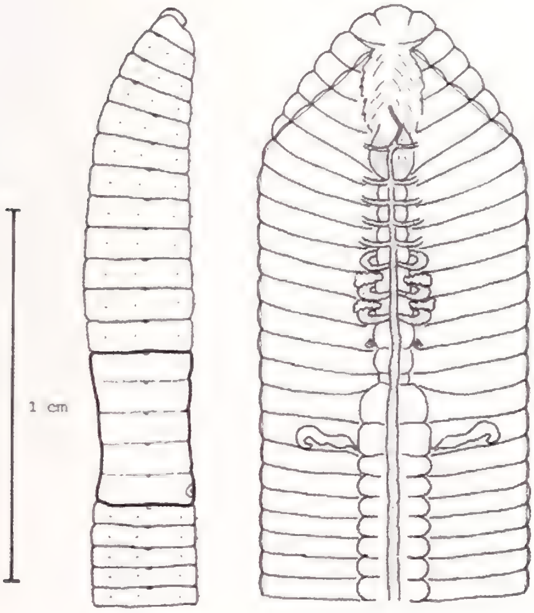

Fig. 2. *Microscolex dubius*. External morphology (lateral view); General dissection of the anterior region.

Habitat spectrum. It is common in anthropized biotopes in the basal belt below 300 m asl (gardens, parks, greenhouses, tropical fruit plantations), and also often found in the medium altitude zones (400–600m) occupied by traditional agriculture, and even in the native forests (Canary pine, and laurel forest). Nevertheless, it was not found in the high mountain zones where the extensive lava fields present a practically insurmountable natural barrier (Teide National Park, at altitudes over 2000 m). *M. dubius* has been found throughout the northwest of Tenerife, La Palma and Hierro, being less common on south-facing slopes, mainly in areas lying leeward of the trade-winds (Fig. 1). The presence of this species in Tenerife is note-worthy over deforested or tree-covered biotopes on northern slopes, whereas it diminishes gradually towards the south, which explains the smaller number of specimens found there, due to the dry gritty soil, as well as to the tremendous impact of urban expansion associated with tourism. This is repeated on the south slopes of La Palma, and Hierro, where the habitat range of *M. dubius* is restricted to valleys and ravines, gardens, and avocado, tomato and banana plantations. It also inhabits the deep gorges running through Garajonay National Park (Gomera), and remote areas of Taburiente National Park (La Palma), where it found underneath stones and rotting trunks together with *Dendrodrilus rubidus* and *Eisenia eiseni*.

Chorology. TENERIFE: Santa Cruz–La Laguna metropolitan area; above Las Mercedes laurel forest and La Esperanza pine forest; north-northwest slopes from the towns of Acentejo to Icod, Daute and Santiago del Teide; south to southwest slopes from the Malpais of Candelaría-Valle de Güimar, to Chasna, Abona and Adeje. LA PALMA: Metropolitan area of Santa Cruz, rural center of Mazo, and Las Breñas; northwest districts between the disperse evergreen laurel forest of Cueva del Agua and conifers around Puntagorda; northeast districts from the antropized zones of Puntallana to the undisturbed laurel forest of Cancelitas; villages of Valle Aridane, and dispersed pine forest in the southern district of Fuencaliente. GOMERA: Woodlands on the central plateau of El Cedro; agricultural areas on the northwest slopes (Vallehermoso and Valle Gran Rey. HIERRO: Metropolitan area of Valverde; deforested soils on north slopes between Nizdafe; El Pinar (Barranco de la Vieja, 28RBR0667)); wide forested bands in Las Dehesas, Julán, and Tajace.

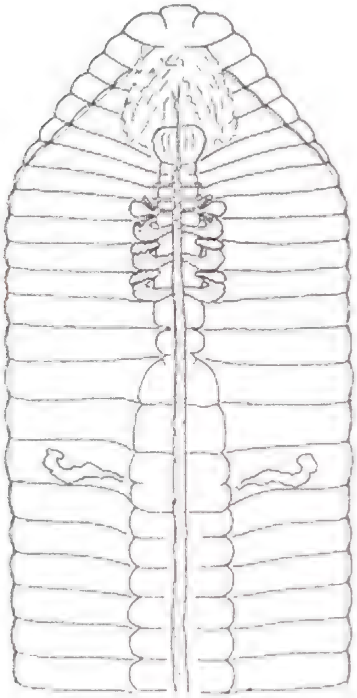

Fig. 3. *Microscolex phosphoreus*. External morphology (lateral view); General dissection of the anterior region.

Microscolex phosphoreus (Dugès, 1837)
Lumbricus phosphoreus Dugès, 1837
Microscolex phosphoreus Bouché, 1972

Remarks. The body length between two and 5.5 cm (average 3.4) is evidence that the Canary island specimens are smaller than those described from continental areas. In addition, it differs from *M. dubius* in its smaller size, genital papillae in segment 11, penial chaetae present in 17, and a pair of diverticulate pyriform (pear-shaped) spermathecae in segment 9. *M. phosphoreus* is recorded for the first time from Hierro.

Habitat spectrum. We consider *M. phosphoreus* a species indicative of agricultural activity, whose pattern of habitats is tropical fruit crops by drip-feed irrigation and cultivated areas subject to the use of fertilizers. It was occasionally found in gardens with exotic plants and deforested sites up to 1500 m, sharing ecological niches with *M. dubius*. This species has a fragmentary distribution clearly related to human action; it is present on all the western Canary Islands, Gomera contributes the least number of specimens whereas Tenerife the greatest number, mainly in the northern zone in banana and avocado plantations. It is quite scarce in the South, where it arrived accidentally in soil transported from the northern slope to improve the ground used for tropical fruit and tomatoes. In La Palma, *M. phosphoreus* is noteworthy in some horticultural areas near the port and a few rural towns and villages in the basal belt, where produce for export is grown by irrigation. On the other hand, this species prefers the pineapple, banana and avocado plantations at the northeastern end of Hierro, whereas its presence on Gomera is restricted to the bay of San Sebastián and its suburbs, which suggests recent colonization and incipient populations of *M. phosphoreus* with little capacity to expand towards other sites.

Chorology. TENERIFE: Parks in Santa Cruz; Botanical Garden above Puerto de la Cruz; anthropized biotopes on the north slopes (from La Victoria of Acentejo to Los Silos), and south to southeast (Arona - Adeje).LA PALMA: Around the port of Santa Cruz de la Palma; vegetable gardens in Las Breñas districts; and fragmentedly in the Valle Aridane area; Barlovento (northeast); Garafía, (northwest). GOMERA: Metropolitan area of San Sebastián. HIERRO: cultivated plots with non-native crops in Valverde; adjacent hamlets with farming tradition; Dehesa (northwest); southeast of El Pinar (Barranco de la Vieja, 28RBR0667).

4. DISCUSSION AND CONCLUSIONS

This new contribution, as did the earlier study (Talavera 1990b, 1992b), adds to the knowledge of these earthworms widely distributed over tropical America and Africa. The family Acanthodrilidae Claus, 1880, is made up of more than twenty genera (Sims 1980), of which *Microscolex* has been able to reach the western Canary Islands but with unequal success, the seaports being the main entry point of *M. dubius* and *M. phosphoreus*. This latter species was introduced by man in recent times, perhaps from the 18th century on, as a result of the increase in foreign trade and imports of exotic plants from the Caribbean colonies and Latin America. However the colonizing process of M. *dubius* may have begun in more remote times, as shown by its presence deep within the native forests in the Canaries. In any case, both peregrine species initially used empty niches free of predators and native parasites, which favoured the installation of pioneer individuals in a short period of time. This hypothesis is in agreement with Gates (1972) for European lumbricids transported to America by man. Fig. 1 reveals some differences at the chorological level, for example that *M. dubius* is more abundant than *M. phosphoreus*. In fact, the latter is restricted to tropical fruit plantation parks and gardens with exotic plants imported from America.

The habitat spectrum of *M. dubius* is wider, it was even found in the native *Pinus canariensis* and evergreen laurel forests, where it may constitute independent populations, or otherwise occasionally share its ecological niche with epigeous lumbricids or the endogeous species *Al-*

lolobophora chlorotica Savigny, 1826 belonging to the ancient fauna of the Canaries. Indeed, no indications of interspecific competition among them were detected, which concords with what ABBOT (1982) reported for Western Australia. We suggest three reasons why *M. dubius* has prospered more than *M. phosphoreus*: ecological plasticity, mode of transportation, and the colonization period; since *M. dubius* has been able to adapt to a greater diversity of habitats, use other dispersion routes besides the merely human one, and its colonization process began long ago, as testified by finding it in montane zones with difficult access. All this is compatible with the possible advantage that would be provided by parthenogenesis in recently colonized sites, where the probability of finding a mate is less.

KRAEPELIN (1895) in his naturalist study cites *Microscolex poulteni* Beddard, without mentioning number of specimens, locality, or which island. However, all the collected indications and data lead us to remove it from the present Canary Islands catalogue of valid species, as well as from any list of species ‘to be confirmed’ or considered as extinct, simply because it did not exist nor has it been introduced into the Canary Islands. We suspect that the researcher K. Kraepelin, inexpert in earthworm taxonomy performed an imprecise identification, perhaps due to the similarity between *M. poulteni* and *M. dubius*. Besides this, it is unlikely that this latter peregrine species could have been passed by unnoticed, since it is the only acanthodrilid with a wide distribution in the Canary Islands. In general the *Microscolex* genus is scarcely represented in the Atlantic islands, which contrasts with its wide continental presence. In particular, when comparing our results with those obtained in Madeira (TALAVERA 1996), the same is confirmed (only two species: *M. dubius* and *M. phosphoreus*), showing similarities between the habitat preferences and distribution range of both. The colonization process in the Canaries and Madeira probably followed the same pattern, mainly as regarding the role of human activity and the routes along which these acanthodrilids became dispersed over the basal and montane belts, where we consider that the easy altitudinal movements of bird flight were one of the possible modes of transport of cocoons-larvae (adhered to legs or plumage). This hypothesis is supported by other authors, among them TERHIVUO (1988) suggested it as a pathway in the colonization of oceanic islands.

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Biting Midges of the Genus *Palpomyia* Meigen (Diptera: Ceratopogonidae) in India

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Abstract. The Indian species of *Palpomyia* Meigen are revised with the addition of two new species, *P. pseudorivularis* and *P. simplitheca* and two new records of *P. magna* Tokunaga and *P. stella* Tokunaga previously described from New Guinea. The species *P. flexidigita* Sinha et al. and *P. novita* Saha & Das Gupta are proposed as new synonyms of *P. crassipalpis* Sinha et al., and *P. barbara* Saha & Das Gupta is considered here as a new synonym of *P. deminutipalpis* Sinha et al.

Keywords. Diptera, Ceratopogonidae, *Palpomyia,* new species, synonyms, India.

1. INTRODUCTION

Palpomyia was established as a genus by Meigen (1818) (as a synonym of *Ceratopogon* Meigen) with the single type species, the European *Ceratopogon flavipes* Meigen. Edwards (1926) divided the genus into three groups on the basis of the number of spines and the degree of swelling of the fore femora. Grogan & Wirth (1975) recognized four distinct groups based on a combination of morphological features.

The larvae of *Palpomyia* are an important source of food for fishes preying on zoo benthos (Remm 1976) and are utilized as indicators of water quality on account of their response to certain types of pollution (Grogan & Wirth 1979). According to Borkent & Wirth (1997) and updated by Borkent (2008), there are 264 extant species, including nine Indian species: *Palpomyia albiditarsis* Kieffer 1910, *P. himalayae* (Kieffer, 1911), *P. leucopogon* Kieffer 1911, *P. rivularis* Kieffer 1911, *P. crassipalpis* Sinha, Das Gupta & Chaudhuri 2003, *P. deminutipalpis* Sinha, Das Gupta & Chaudhuri 2003, *P. flexidigita* Sinha, *P. barbara* Saha & Das Gupta 2005, and *P. novita* Saha & Das Gupta 2005.

This paper presents a revision of the Indian species of *Palpomyia* including two new species and new records of two species previously known only from New Guinea. *Palpomyia flexidigita* and *P. novita* are proposed as new synonyms of *Palpomyia crassipalpis* and *P. barbara* as a new synonym of *Palpomyia deminutipalpis*. Thus, the total number of valid species of *Palpomyia* in India adds up to ten.

2. MATERIAL AND METHODS

The insects were collected with light traps at different localities in West Bengal, India. They were cleared and mounted in a mixture of phenol and Canada Balsam on microscope slides after appropriate orientation. Morphological terminology used in the species descriptions mostly follows Giles & Wirth (1984) and Bose et al. (2003). Types and identified specimens are housed in the Insect collections of the Entomological Laboratory of the University of Burdwan and will be submitted to the National Zoological Collections (NZC), Calcutta.

3. TAXONOMY

Key to Indian species of *Palpomyia* Meigen

* Kieffer types are considered lost, hence types of these species were not seen and the species names may be nomina dubia.

1. Wing membrane pale brown to grayish 2
   Wing membrane hyaline 7
2. Scutum with short anteromedially bristles and without
   tubercle 3
   Scutum without any bristles anteromedially and with
   tubercle 4
3. Male with narrow sternite IX having a deep caudo median excavation
   Gonostylus short, bud-like, with a blunt end
   .... *crassipalpis* ♂

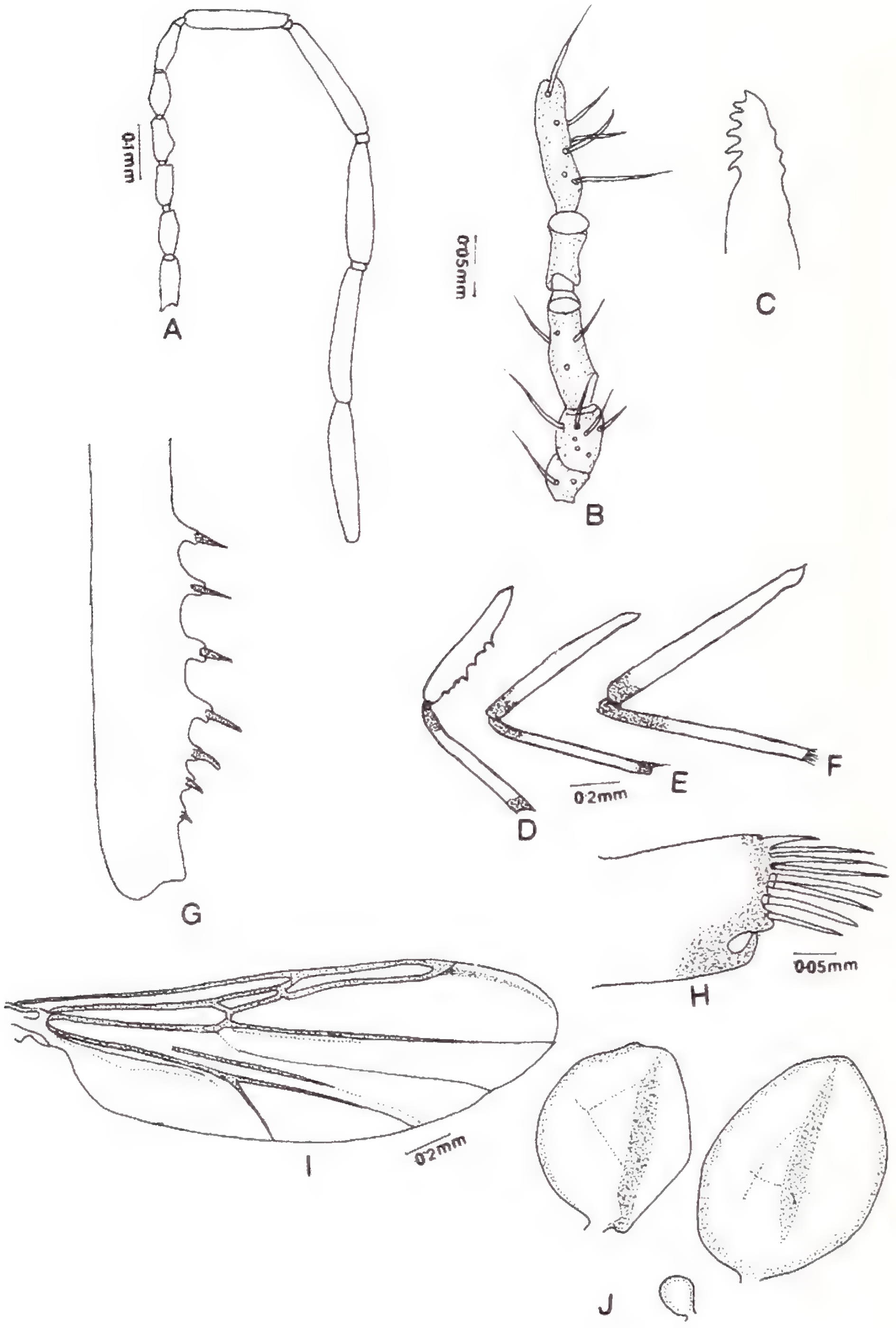
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Fig. 1. A–J. *Palpomyia pseudorivularis* sp.n. ?. A) antenna, B) Palpus, C) Mandible, D–F) fore, mid, hind femora and tibiae, G) spines on fore femur, H) hind tibial comb, I) wing, J) spermathecae.

Male with a broad sternite IX, without caudomedian excavation. Gonostylus slender, with a hooked tip .... *deminutipalpis* ♂

4. Mid and hind femora with dark brown apical bands. Mid tibia with one apical spine 5
Mid and hind femora pale, without pigmented bands. Mid tibia without apical spine 6
5. Palpal segment III of female with a subapical pit with two sensillae. Palpal segment V with a long apical spines .... *implitheca* ♀
Palpal segment III of female without sensillae. Palpal segment V with a short subapical spine .... *pseudorivularis* ♀
6. Female with inflated forefemur bearing 8–10 ventral spines on entire length .... *magna* ♀
Forefemur slender in both sexes, with 3 and 4 apical spines, respectively .... *stella* ♂, ♀
7. All femora of male armed with stout spines .... **leucopogon* ♂
Only fore femora armed with stout spines 8
8. Female thorax shining red, bearing a pair of mediolateral spinules .... **himalayae* ♀
Female thorax either dark brown or black and devoid of spinules 9
9. Female dark brown with pale halter .. **albiditarsis* ♀
Female with a deep black body and dark brown halter ....**rivularis* ♀

Descriptions of the species

Palpomyia crassipalpis Sinha, Das Gupta & Chaudhuri, 2003 (Sinha et al. 2003: 75).
Palpomyia flexidigita Sinha, Das Gupta & Chaudhuri, 2003: 79. **New synonym.**
Palpomyia novita Saha & Das Gupta, 2005: 63. **New synonym.**
♀: Unknown.

Material: Holotype ♂, West Bengal, Panagarh Agriculture Farm, 20.vi.1990. leg. P. K. Chaudhuri. 2 ♂, Durgapur, 13.vii.2001, leg D.Sai; 1 ♂, Asansol, 18.viii.2001, leg. S. Sen.

Remarks. Sinha et al. (2003) described the species from India. The midges in the present study conform fully with those of the above authors and the holotype of *P. crassipalpis.* After critical study and a comparison of *Palpomyia flexidigita* and *P. novita* with *P. crassipalpis* it has been concluded that these species are synonymous with *Palpomyia crassipalpis*. In this context, it should be noted that Fig.1 of *P. crassipalpis* was mistakenly printed as Fig. 3 of Sinha et al. (2003).

The species may be diagnosed by the following combination of character states: short palpal segments, anterior part of thorax hairy, 5 bristles on the scutellum, femora with dark brown broad apical band, hind tibia dark brown with pale band at its apical 1/3rd, 5 forefemoral spines, 9 spines of hind tibial comb, thumb like hind tibial spur, grayish wing about three times longer than broad, r_2 1.5 times longer than r_1, aedeagus with longer recurved basal arms and slender distal arm, parameres fused and slender gonostylus ending with a bud

Palpomyia deminutipalpis Sinha, Das Gupta & Chaudhuri, 2003 (Sinha et al. 2003: 79).
Palpomyia barbara Saha & Das Gupta, 2005: 62. **New synonym.**
♀: Unknown.

Material. 3 ♂, West Bengal, Asansol, 23.vii.2001, leg. G. Bhattacharyay;1 ♂, Kumardubi, 25.vii.2001, leg. D. Sai. Holotype ♂, Belpahari, 8.vi.1991, leg. S. Sinha.

Remarks. The present specimens conform with those of Sinha et al. (2003) in structures and the morphometrics. The diagnostic features of the species are: elongated palpal segment II with sensory pit, reduced palpal segment V, scattered hairs and streak on thorax, 7 fore femoral spines, hind tibial comb of 7 spines, r_2 little longer than r_1, elongated gonocoxite with broad base, short gonostylus with bud at the tip, triangular aedeagus having deep median excavation and heavily sclerotized parameres with fused basal arms

On examination of the types and previous description of Sinha et al. (2003), it appears that *Palpomyia deminutipalpis* and *Palpomyia barbara* are the same species and *P. barbara* is proposed as a new synonym of the former species due to similarities of morphological features as stated above.

Palpomyia magna Tokunaga, 1966
(Tokunaga 1966: 130).
Material: 2 ♀, West Bengal, Jorebanglow (2040m), 21.vii.2001, leg. U. Majumdar; 1 ♀, Tindharia (1320 m) 25.vii.2001, leg. S.K. Pradhan.

Remarks. Tokunaga (1966) described the female of the species from New Guinea. In the course of the present study, three insects of the Himalayas are identified as conforming fully to the description by Tokunaga (1966). The species may be diagnosed by: eyes separated as wide as one facet, 12 (6 large and 5 minute) mandibular teeth, scutellum with 4 large and many small bristles, fore femur mostly with 10 spines, hind tibial comb of 8 spines,

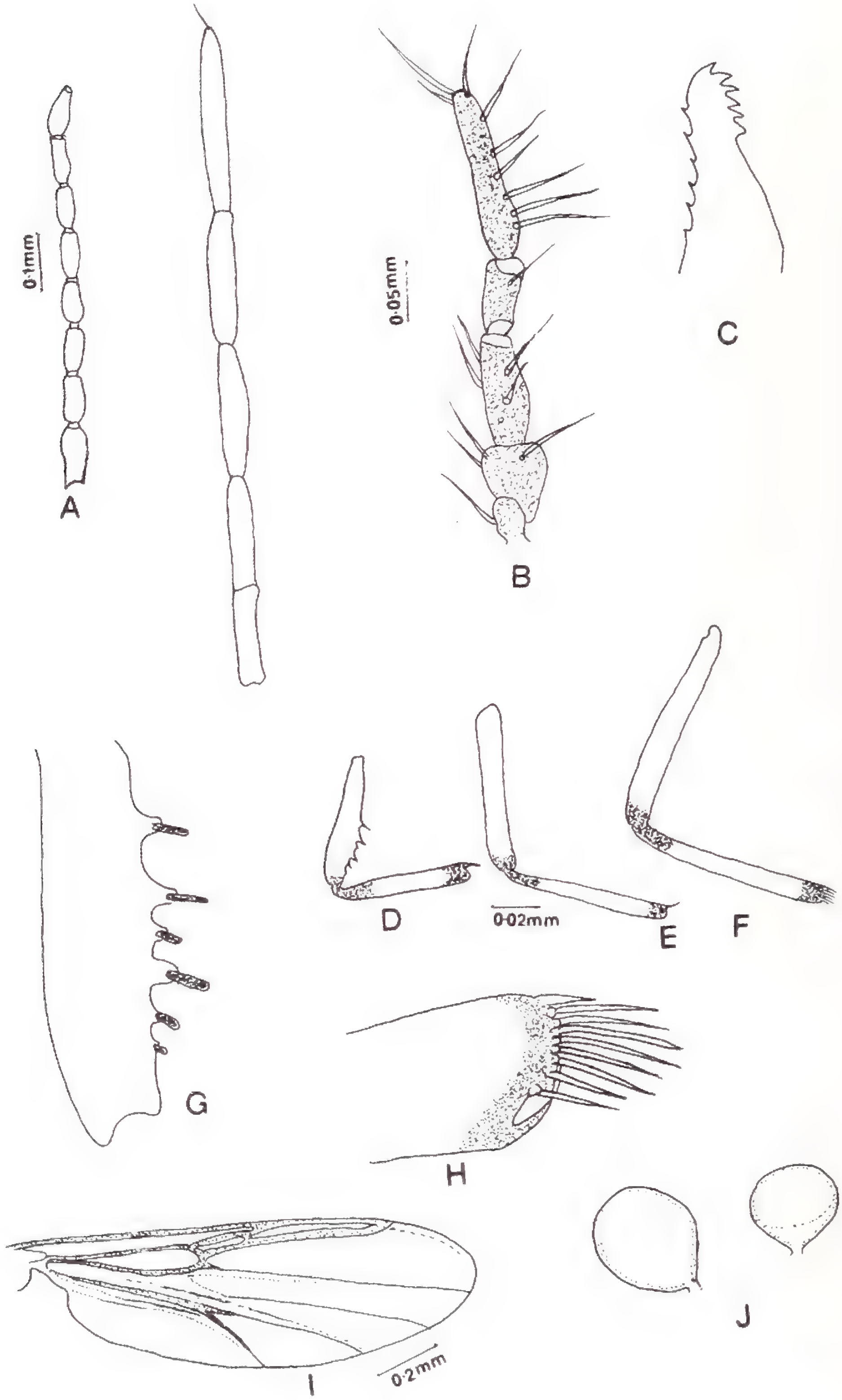
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Fig. 2. A–J. *Palpomyia simplitheca* sp.n. ?. A) flagellomeres I–XIII, B) Palpus, C) mandible, D–F) fore, mid , hind femora and tibiae, G) spines on fore femur, H) hind tibial comb, I) wing, J) spermathecae.

wing pale with brown apical part, r-m shorter than ♂ of the base of Rs and M, abdomen ochreous with pale bands on segments I–IV, dark brown bands on segments V–IX, small gland rod and two sub equal oval spermathecae.

Palpomyia pseudorivularis Das Gupta, sp. n. (Figs 1A–J)

♀. Head. Eyes separated completely. Antenna (Fig. 1A) with flagellomeres I–VIII yellow at bases, IX–XIII completely brown with pale bases and 2x length of VII; lengths of flagellomeres I–XIII 8: 5: 5: 5: 5: 5: 5: 6: 10.5: 13.5: 14.5: 16: 18.5, AR (Antennal ratio) 1.65. Palpus (Fig. 1B) uniformly brown, palpal segment III with apical sensory pit, segment V elongated bearing a sub apical spine; length ratio of palpal segments I–V 3: 4: 7: 5: 10, PR (Palpal ratio) 3.0. Mandible (Fig. 1C) with 6 strong teeth.

Thorax. Brown, very hairy with small blunt anterior tubercle, scutellum pale, with 8 large and many small bristles.

Legs (Figs 1D–F). Coxae brown, trochanters yellow, fore femur (Fig. 1G) with 7 stout spines, mid and hind femora with dark brown apical band, tibiae with dark brown basal and apical bands, mid tibia with 1 apical spine, tarsomeres I–II light yellow, III light brown, IV–V totally brown, mid tarsomeres I–II with 2 apical spines; length ratio of leg segments 23:19: 8: 4: 2.5; 2: 3 in fore leg, 28: 23: 12: 4: 2: 1.5: 2.5 in mid leg, 32: 27.5: 14: 7: 2.5: 2:3.in hind leg. TR (Tarsal ratio) of hind leg 2.0. Hind tibial comb (Fig. 1H) with 7 spines.

Wing (Fig. 1I): Wing length 2.85 (2.84–2.85, n=4), wing breadth 1.05 (n=3) mm. Membrane light brown with brown veins, R_{4+5} ending well beyond the middle, r_2 2.33 times longer than r_1 (21:9), costal length 2.31mm; CR (Costal ratio) 0.81. Halter brown.

Abdomen. Tergites brown, cerci brown, gland rods distinct. Spermathecae (Fig. 1J) large, unequal, 0.18 x 0.12 and 0.14 x 0.10 mm, and the third rudimentary distinct.

Material. Holotype ♀, Darjeeling (2180m) 20.x.1978, leg. Sikha Sarkar. Paratypes 2 ♀, Darjeeling, 12.ix.2002, leg. A. Mazumdar.

Remarks. Due to its relatedness to *P. rivularis* Kieffer, 1911, the species is named *P. pseudorivularis*. It resembles *P. rivularis* Kieffer in the shape of the flagellomeres, tarsomere I and structure of the spermathecae. The color pattern of the hind tibia and the femoral spines of *P. subspara* (Coquillett, 1901) and *P. tainana* Kieffer, 1912 are somewhat similar to those of the new species, but the following character states are distinctive:, dark palpal segment III with an apical pit, 6 strong teeth of mandible, very hairy thorax, 8 bristles on the scutellum, dark brown color band of hind tibia, 6 stout femoral spines, 7 spines of hind tibial comb, length of r_2, dark brown halter knob, distinct gland rod, structure of spermatheca and distinct rudimentary spermatheca.

Palpomyia simplitheca Das Gupta, sp. n. (Figs 2A–J)

♀. Head. Eyes separated as widely as 2 facets. Antenna (Fig. 2A) with flagellomeres I–VIII yellow basally, apically brown, IX–XIII brown with pale bases and almost equal or longer than VIII; length ratio of flagellomeres I–XIII 8 : 5 .5 : 5 : 5 : 5 : 5 : 5 :5 :10 : 12 : 12.5 :13.5 : 18, AR 1.52. Palpus (Fig. 2B) uniformly brown; palpal segment III with a sensory pit having 2 sensillae, segment V long with a long stiff spine in addition to normal two; length ratio of palpal segments I–V 2.5: 4: 6.5: 4.5: 10, PR 3.25. Mandible (Fig. 2C) with 6 large strong teeth.
Thorax. Dark brown with a few anterior hairs and a small blunt anterior tubercle, scutellum pale with 4 large and several small bristles.

Legs (Figs 2D–F). Coxae brown, trochanters yellow, fore femur (Fig. 2G) with 6 short and stout apical spines, mid and hind femora with dark brown apices, tibiae with dark brown basal and apical bands, color band of hind tibia narrow, tarsomeres I–II pale yellow, III little brown, IV–V brown; length ratio of leg segments 18.5: 16.5: 8: 3: 2: 1.5: 3 in fore leg, 23: 20: 11: 3: 2: 1.5: 2.5 in mid leg , 28: 24: 13: 5: 2: 1.5: 3 in hind leg. TR of hind leg 2.6. Hind tibial comb (Fig. 2H) with 8 spines.

Wing (Fig. 2I). Wing length 2.38 (2.35–2.39, n=4), wing breadth 0.84 (0.84–0.85, n=4) mm. Membrane light brown, R $_{4+5}$ ending well beyond the middle, M_2 arising before r-m cross vein; r_2 2.35 times longer than r_1, costal length 1.93 mm. CR 0.8. Halter brown with light brown knob.

Abdomen. Tergites brown, cerci brown. Spermathecae (Fig.2 J) simple, small, unequal, 0.091 by 0.067 mm and 0.076 by 0.062 mm.

Material. Holotype ♀, Darjeeling, 23 .VII.1968, leg. S.K. Das Gupta.

Paratypes 2 ♀, Darjeeling, 23, vii. 1968, leg. S. K. Das Gupta; 1♀, 28.vii.2001, leg. U. Majumdar.

Remarks. The species is named *P. simplitheca* due to the simple spermatheca. In the number and nature of mandibular teeth, the wing, and the spermathecae, the species resembles the females of *P. flaviceps* (Johannsen, 1908) and *P. jimmensis* Tokunaga, 1966. The color pattern of legs of the new species and of *P. lineata* (Meigen) appears more or less similar. It appears to be closer to *P. pseudorivularis* but the following combination of character states is unique: flagellomeres IX–XI brown at base, yellow at the apices and almost equal in length to flagellmere VIII, 6 large teeth of the mandible, thorax with a few anterior hairs and a small blunt anterior tubercle, 8 large bristles and several small bristles on scutellum, color pattern of femora and tibiae, narrow color band on hind tibia, 8 spines on hind tibial comb, length of r_2, and a simple, small spermatheca

Palpomyia stella Tokunaga, 1966
(Tokunaga 1966: 136).

Material. 3 ♂ 2 ♀, Burdwan, 17.vi.1999, leg. P.K.Chaudhuri; 2 ♂, 2 ♀, Durgapur, 12.v.2000, leg. D. Sai; 1 ♂, Uttarapara, 01.viii.2001, leg. U. Majumdar; 1 ♂, Chinsura, 21.vii.2003, leg. D. Sai

Remarks. Tokunaga (1966) originally described this species from New Guinea and New Britain. A few biting midges in our study are identified as *Palpomyia stella* because they appear indistinguishable. The species may be identified by the following combination of characters: small size, very pale ochreous palpus, swollen segment III, presence of conical scutal tubercle, scutellum with 4 long bristles and 15 short bristles, absence of definite color pattern on legs, 3 spines on fore femur, 3 spines on the hind tibial comb, pale wing with C extending beyond the end of R_{4+5}, r_2 2.25 times longer than r_1, slender and tapered gonocoxite, gonostylus swollen arched, with 3–4 small setae, trapezoid aedeagus, fused parameres with star-like median lobe little longer than basal arms and the tip rounded, bearing barb-like hook; female abdominal tergites I–II with pale median linear stripes, absence of gland rods and presence of two unequal oval spermathecae.

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Second Find of the Recently Discovered Amazonian Giant Peccary, *Pecari maximus* (Mammalia: Tayassuidae) van Roosmalen et al., 2007: First Record from Bolivia

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Abstract. We report on the discovery of a large peccary in the Amazon rainforest of northwestern Bolivia in the area of "Bolpebra" close to both the Peruvian and the Brazilian border, which is documented by several photographs. Its size, the relatively small head, long legs, and relatively thin and short fur without white-coloured markings leave no doubt that this is the second find of the Amazonian giant peccary, *Pecari maximus*, which was first discovered and described from Rio Aripuana, Amazonian Brazil, by VAN ROOSMALEN et al. (2007). Our second record for the species is at the same time the first for Bolivia, and the close geographic proximity to SE Peru makes its occurrence in this country also very likely. We suggest that this unique giant peccary should serve as a flagship species for protecting the entire region of its potential distribution range in a frontier-crossing World Heritage Site.

Keywords. *Pecari maximus*, Bolivia, Amazon rainforest.

1. INTRODUCTION

Only few years ago, a giant peccary species was discovered in Amazonian Brazil, the fourth species in the Neotropical artiodactyle family Tayassuidae (VAN ROOSMALEN et al. 2007). Being the largest of the four extant peccary species, it was named *Pecari maximus*. First molecular data showed that it is the sister species of the collared peccary (*Pecari tayacu*), while the white-lipped peccary (*Tayassu pecari*) and the Chacoan peccary (*Catagonus wagneri*) form the sister clade of the two former. The description of *P. maximus* was one of the spectacular discoveries of a new large mammal species and took place only three decades after the discovery of another Neotropical pig, viz. *Catagonus wagneri*. The latter species had originally been described as a fossil taxon, and later it was discovered to survive in the Chaco of Paraguay (WETZEL et al. 1975; WETZEL 1977 a, b, 1981). This (re)discovery was long preceded by information provided by Carl BERKHAN, a German farmer resident in the Bolivian Chaco, who reported to M. EISENTRAUT in 1930 on the existence of a third and even fourth peccary species in the Chaco (see EISENTRAUT 1986; BÖHME & HUTTERER 1999; BÖHME & STIELS 2007). Only six decades later the presence of *C. wagneri* was proven also in Bolivia, one decade after its initial discovery as a living taxon in Paraguay (EISENTRAUT 1986). In the case of *P. maximus* from Amazonian Brazil, it took only two years since its discovery before it was also found in a neighbouring country. This sighting was made in 2005 and is reported and discussed below.

2. COMPARATIVE DESCRIPTION OF A BOLIVIAN SPECIMEN OF *PECARI MAXIMUS* WITH SOME ECOLOGICAL NOTES

In January 2005, the senior author spent 16 days in a remote area of the Bolivian side of the triangle where Bolivia, Peru and Brazil meet ("Bolpebra"). Close to a settlement named Bioceanica (11°08'S, 69°22'W), local hunters had killed an obviously young female peccary which was subsequently skinned, and some photographs were taken for documentation (Figs 1–3). The head-body length of this specimen was approximately 105 cm (the hunter's knife in Fig. 3 measured 38 cm for comparison,). The legs were much longer than in the two sympatric species *P. tayacu* and *T. pecari*, while the head was relatively smaller than in females of these species. The fur was thin, leaving much of the skin visible and showing some dark mottling, but in the neck and middorsal region, the hairs were longer and darker. There was no trace of a white collar typical for *P. tayacu,* nor of whitish lips as in *T. pecari* (rather lighter bristles occurred in the lower part

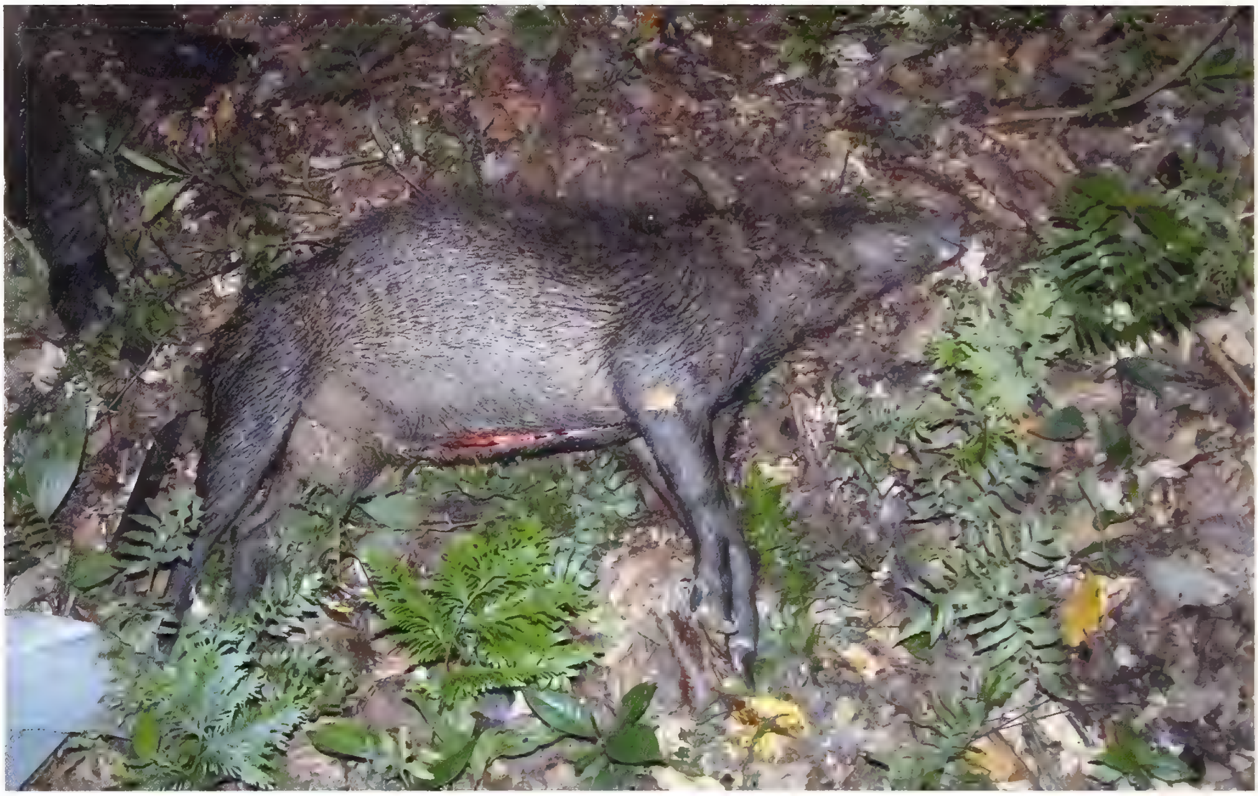

Fig. 1. Young female *Pecari maximus*, shot at Bioceanica, Bolivia. Photograph J. Moravec.

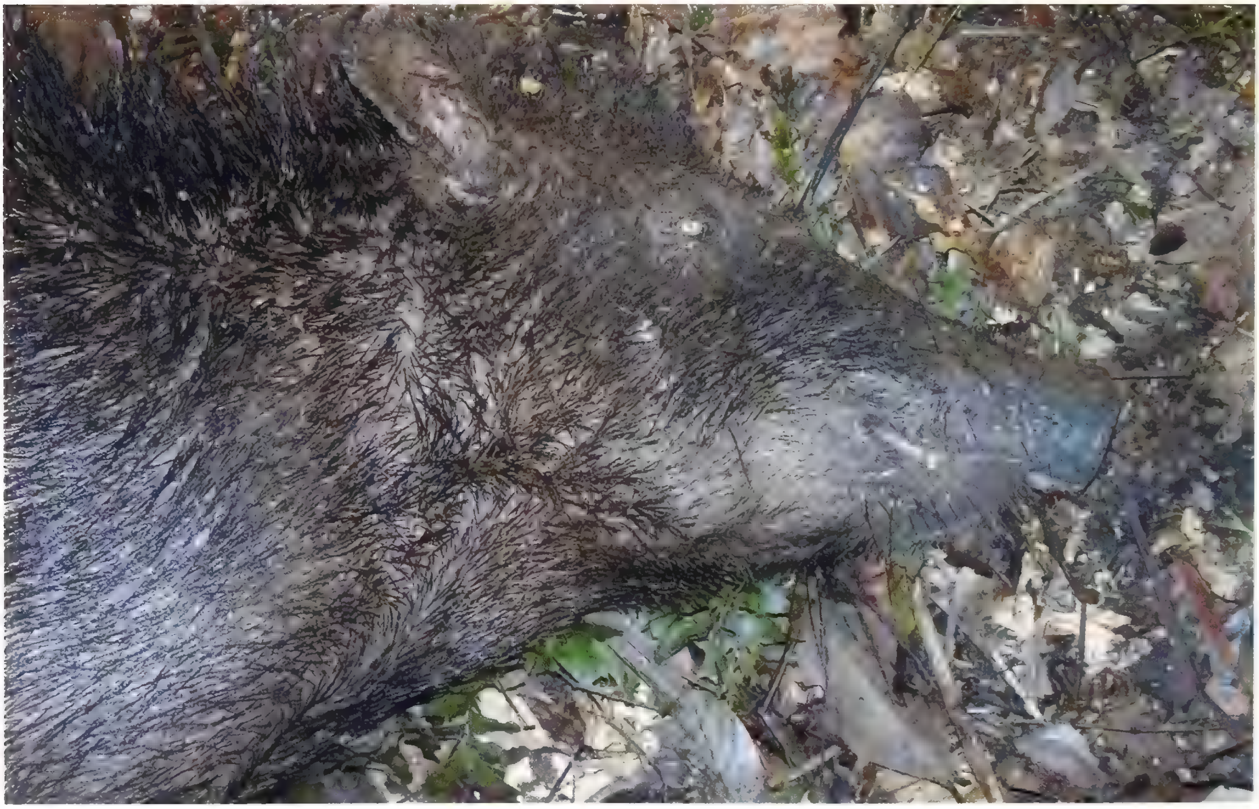

Fig. 2. Lateral view of the head of the same specimen. Photograph J. Moravec.

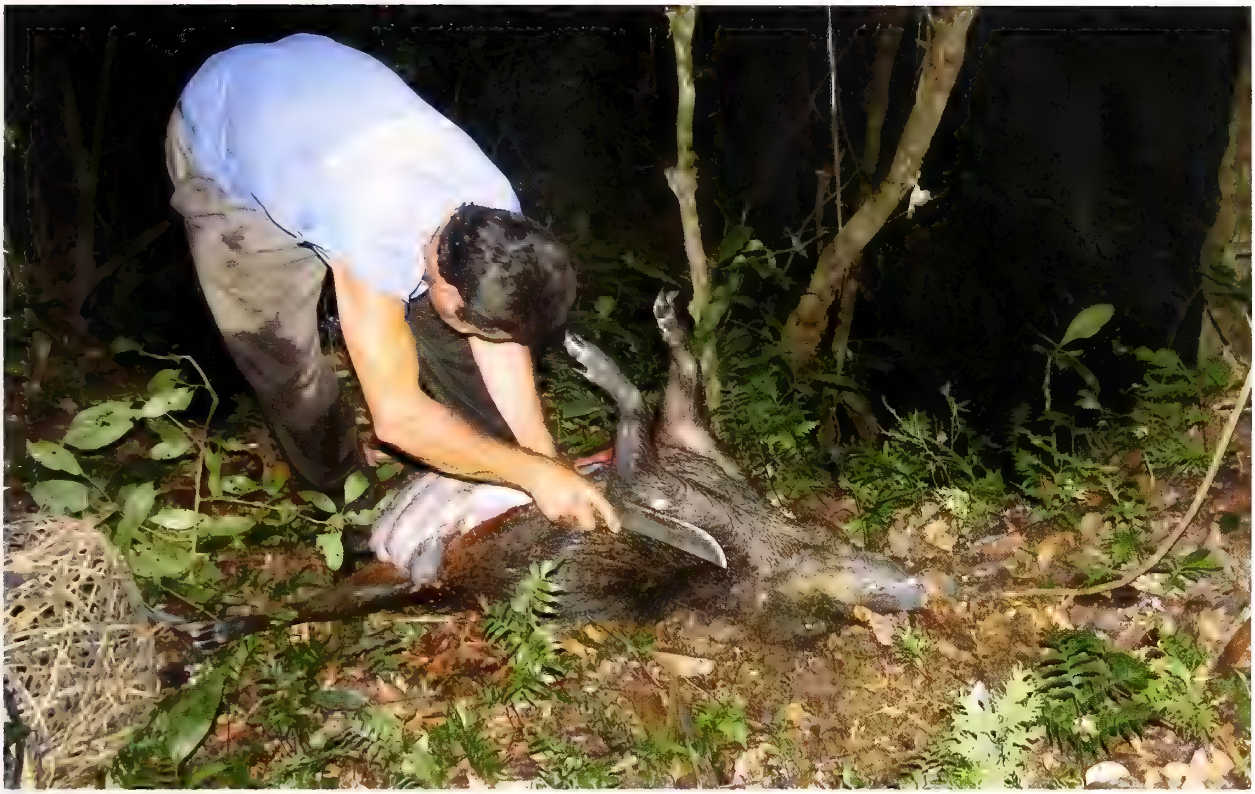

Fig. 3. Local hunter beginning to skin same specimen. Photograph J. Moravec.

of the cheek area only). The brown dark mottled fur colouration differed from the strongly speckled dark blackish-grey fur colouration of *P. tayacu* as well as from the blackish brown longer fur of *T. pecari*. In the figures the differences in fur colour and bristle-haired texture are evident although the freshly killed female pig lay in a forest creek and was therefore wet.

All characteristics given above are diagnostic for *P. maximus* from Rio Aripuana in Brazil, compared with its only congener *P. tayacu* (Fig. 4). It is characterized "in being much larger but less robust, with much longer legs and a proportionally small head only slightly bigger than that of *P. tayacu*. Most of the body is thinly bristle-haired, overall colour brown mixed with dirty white, a black mid-dorsal mane running from the ears as far as the rudimentary tail. Nasal disc pinkish, relatively small and soft" (van Roosmalen et al. 2007). According to this diagnosis, the Bolivian female specimen described here belongs without any doubt to *Pecari maximus* and represents thus the second documented record for this new species. At the same time, it is the first record from outside Brazil, viz. from Bolivia.

The distance between the type locality of *P. maximus* (left bank of the Rio Aparuana, at the mouth of its tributary Rio Arauazinho, 06°16'S, 60°20'W) is about 1000 km away from our new locality (11°08'S, 69°22'W). However, van Roosmalen et al. (2007) cited already an old report by an American rubber cutter, J. C. Yungjohann, who had lived in the Rio Xapuri area from 1906-1919 which is only 80–100 km NE of the Bolivian site at Bioceanica. Similarly as the German farmer in the Bolivian Chaco mentioned above, Yungjohann also reported already one century prior to the "official", zoological discovery on a third species of "bush pigs": "There is a great, big one porcao, they travel in pairs, and are very lively" (Yungjohann 2003). Obviously, this truly cryptozoological information is now proven by the new record of *P. maximus* described here.

Also the characterization of *P. maximus* by Yungjohann as living in pairs fits the information given by van Roosmalen et al. (2007) that this species – in strong contrast to the large herds of both *P. tayacu* and *T. pecari* (Sowls 1984) – lives "in small family groups that consist of an adult pair with or without 1–2 offspring". Also the young female from Bioceanica was, according to the hunters, part of a small group of only four specimens.

The area of Bioceanica is characterized by undulating terrain, with the elevation ranging from ca. 250 to 300 m a.s.l. It is covered by tall, slightly selectively logged *terra firme* rain forest characterized by an abundance of Brazil nut

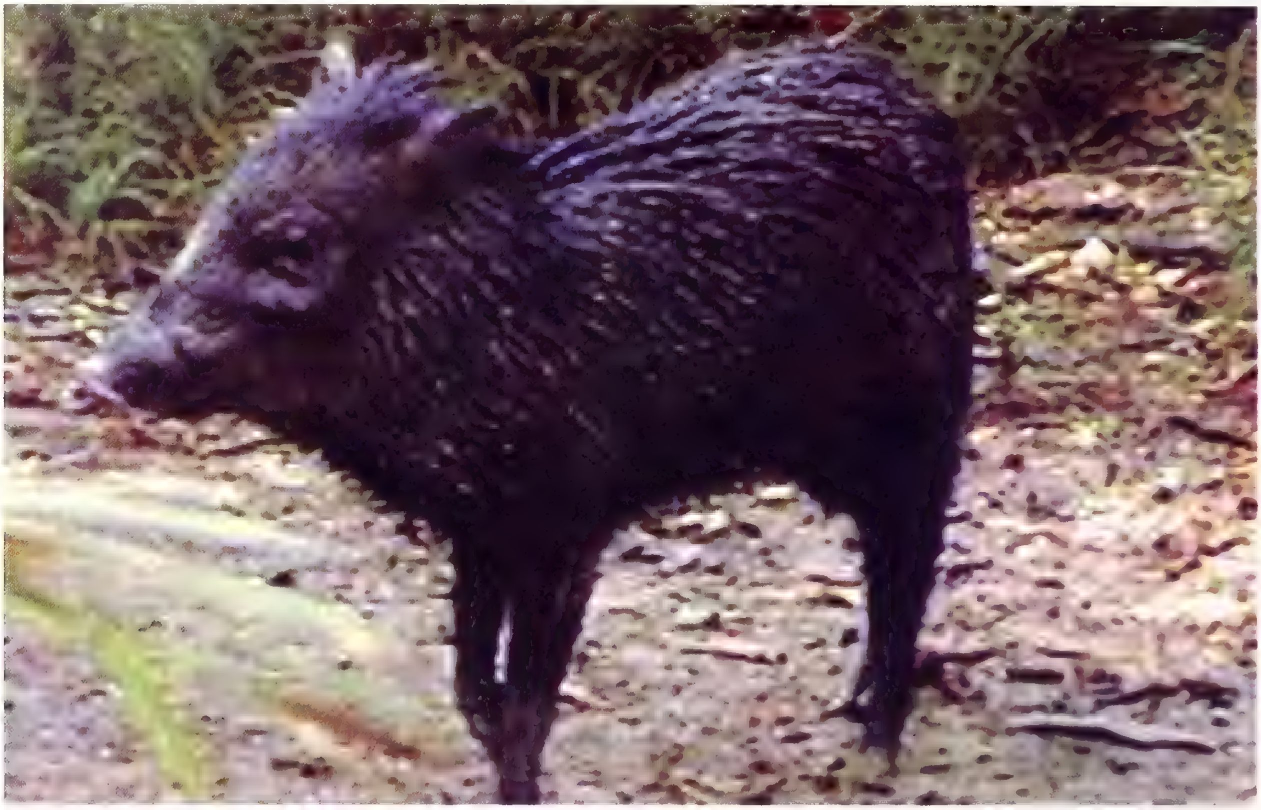

Fig. 4. Live *Pecari maximus* from the type locality. Photograph L. FRENZ.

trees *Bertholletia excelsa*. The upper canopy closes at the height of 30–40 m. The densest understory is associated with moist depressions along forest brooks.

3. CONCLUSION

The assumption by the discoverers of *Pecari maximus* that it might be more widely distributed than known so far has been corroborated by the new, distant find of this species in NW Bolivia. As to its conservation status according to IUCN criteria, it must certainly be regarded as "data deficient". But possible severe threats have already been listed by VAN ROOSMALEN et al. (2007). However, it could well serve as an impressive flagship species for protecting the entire interfluve range between Rio Madeira and Rio Tapajos which yielded several impressive new mammal discoveries and is certainly also full of other, still undescribed vertebrate species. Therefore, we strongly support the appeal by VAN ROOSMALEN et al. (2007) to encourage UNESCO to urge the Brazilian and Bolivian governments to declare the entire region a – frontier-crossing – World Heritage Site, including also the rain forest part of neighbouring Peru.

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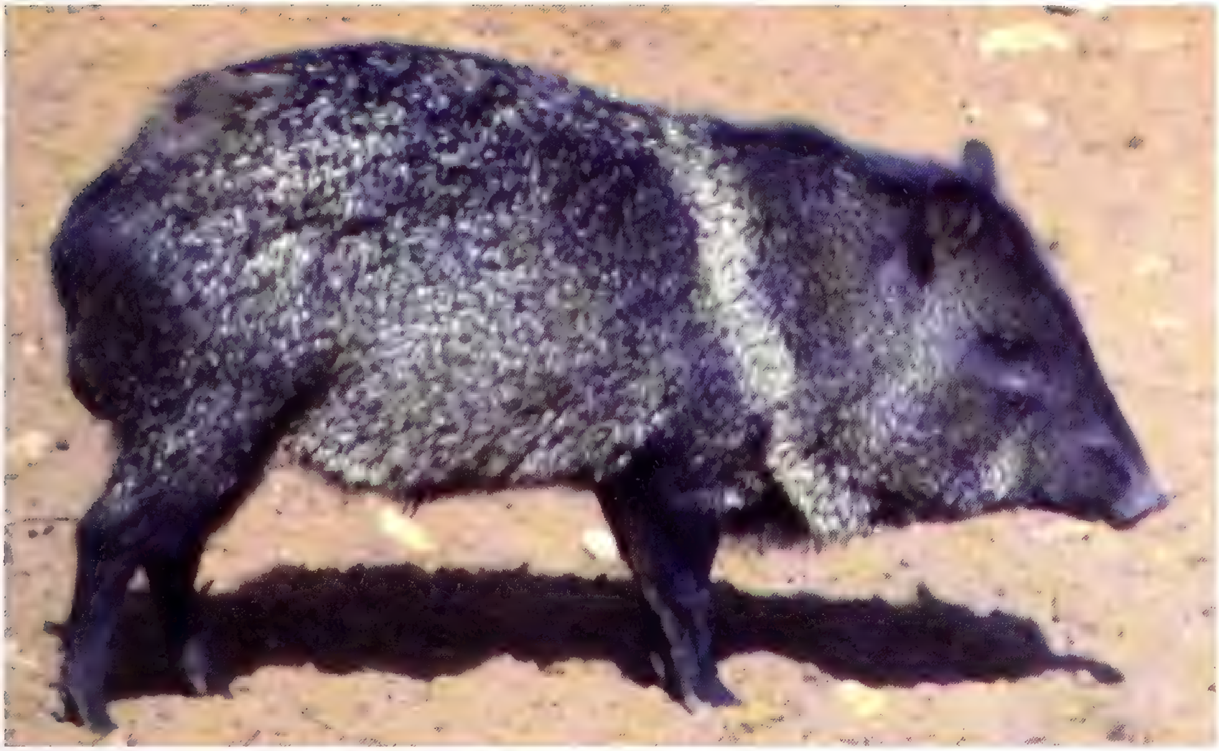
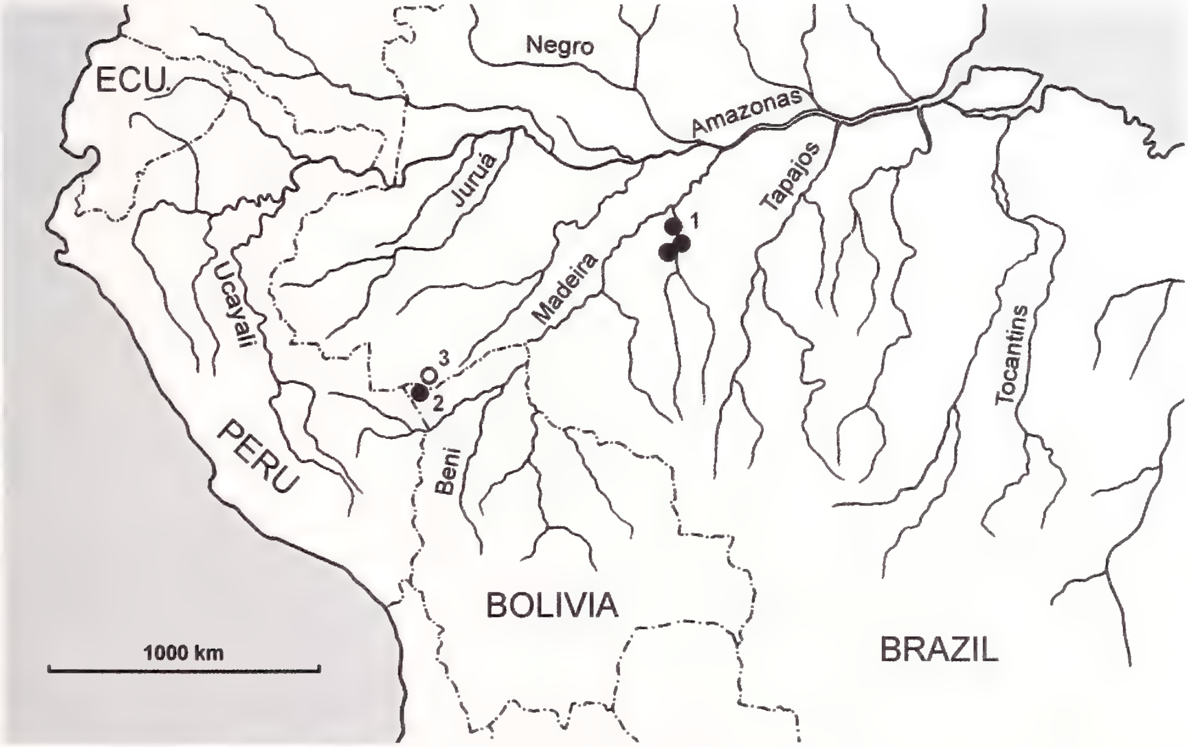


Fig. 5. Live *Pecari tayacu*, congener of *P. maximus* to show the different body proportions. Photograph W. Böhme.


Negro
ECU.
Amazonas
Juruá
Tapajos
1
Ucayali
Madeira
3
2
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PERU
Beni
BOLIVIA
1000 km
BRAZIL

Fig. 6. Map of central South America showing the distribution records of *Pecari maximus*. Drawing J. Moravec.

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On the Phylogeny and Taxonomy of the Genus *Uromastyx* Merrem, 1820 (Reptilia: Squamata: Agamidae: Uromastycinae) – Resurrection of the Genus *Saara* Gray, 1845

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Abstract. We assessed the taxonomic relationships within the genus *Uromastyx* Merrem, 1820 using morphological and genetic methods, resulting in the resurrection of the genus *Saara* Gray, 1845 for *Saara hardwickii*, *S. asmussi* and *S. loricata* and in changes of the taxonomic rank of *Uromastyx nigriventris*, *U. aegyptia leptieni* and *U. shobraki*. A synopsis of all taxa considered to be valid is provided, including differential diagnosis, description and data on their respective distribution. A key for the species of *Saara* and *Uromastyx* is presented.

Keywords. Reptilia; Sauria; Agamidae; Uromastycinae; *Uromastyx*; *Saara*; *Saara hardwickii*; *Saara asmussi* new comb.; *Saara loricata* new comb.; *Uromastyx aegyptia leptieni* new status; *Uromastyx nigriventris* new status; *Uromastyx shobraki* new status; Phylogeny; Taxonomy; Morphology.

1. INTRODUCTION

Within the Palearctic genus *Uromastyx* Merrem, 1820 a total of 17 species are considered to be valid by Wilms & Schmitz (2007) and Wilms & Böhme (2007). Some of the species respective subspecies belonging to that genus have been described quite recently (e. g. *Uromastyx dispar maliensis* Joger & Lambert, 1996; *Uromastyx occidentalis* Mateo et al., 1998; *Uromastyx leptieni* Wilms & Böhme, 2000; *Uromastyx alfredschmidti* Wilms & Böhme, 2001; *Uromastyx y. yemenensis* Wilms & Schmitz, 2007, and *Uromastyx y. shobraki* Wilms & Schmitz, 2007) reflecting a continuing scientific interest in the phylogeny and taxonomy of these animals.

Uromastyx spp. are medium sized to large lizards inhabiting the old world desert belt from North Africa to north western India. All species are either ground dwellers or saxicolous, with some species climbing occasionally on trees. *Uromastyx* are predominantly herbivorous, feeding on the scarce vegetation in their desert environment. Ecologically these animals are largely limited by the availability of food and by the availability of appropriate thermal refuges.

Uromastyx spp. are currently listed on Appendix II of CITES. Internationally more than 367 000 specimens have been traded legally in the pet trade between 1977 and 2005 (Knapp 2004, Wilms 2007a). But the consumption of spiny-tailed lizards in their countries of origin may be considerably higher due to the fact, that *Uromastyx* are heavily hunted for food and for the production of souvenirs and traditional medicine (Wilms 2007a).

The main aim of the present paper is to evaluate the phylogenetic relationships within the taxa of the genus *Uromastyx* and to establish a hypothesis of the taxonomy of this group, based on a synthesis of morphological and genetic characters.

Taxonomic History

The taxonomic history of the lizards currently assigned to the genus *Uromastyx* dates back to the second half of the 18th century [description of *Lacerta aegyptia* Forsskål, 1775; for more detailed information on the history of this taxon see Wilms & Böhme 2000 a. For a discussion on the spelling of Pehr Forsskål's family name see Friis & Thulin (1984)].

The genus name *Uromastyx* was coined by Merrem in his work 'Versuch eines Systems der Amphibien – Tentamen Systematis Amphibiorum' (Merrem 1820). Of the seven species included in this first synopsis of the genus only one is belonging to *Uromastyx* as it is currently defined [*Uromastyx spinipes* (Daudin, 1802) = *Uromastyx aegyptia* (Forsskål, 1775)].

Between 1822 and 1885 a total of five new genera (*Mastigura* Fleming, 1822; *Centrocercus* Fitzinger, 1843; *Saara* Gray, 1845; *Centrotrachelus* Strauch, 1863; *Aporoscelis* Boulenger, 1885) were erected for different members of the genus *Uromastyx* of which only *Aporoscelis* and *Centrotrachelus* were considerably in use (e. g. Anderson 1894, 1896, 1901; Blanford 1874, 1881; von Bedriaga 1879; Murray 1884; Scortecci 1933; Ninni 1933; Parker 1942; Haas & Werner 1969). *Aporoscelis* was used in the rank of a subgenus by Joger (1987). The name *Centrocercus* Fitzinger, 1843 is preoccupied by *Centrocercus* Swainson, 1832 (Aves, Phasianidae) and is therefore not available. The main taxonomic problem within *Uromastyx* was the proper delimitation of taxon boundaries on the specific and subspecific level, which led in the past to considerable confusion on the identity of diverse taxa (for more detailed information see Wilms & Böhme 2000 a, 2000 b, 2001).

Beside studies based on external morphology (e. g. Mertens 1962; Moody 1987; Wilms & Böhme 2000 a, 2000 b; Wilms & Böhme 2001; Wilms & Schmitz 2007) and immunology (Joger 1987), some recent papers also adress this issue by employing molecular genetic methods (Amer & Kumazawa 2005; Wilms & Schmitz 2007; Harris et al. 2007). Nevertheless some aspects of the taxonomy of these highly specialized desert lizards still remain unclear.

On the basis of external morphology and immunological distances it is well established, that several species groups within *Uromastyx* are recognizable, but the relationships and species compositions of these groups are still under debate (Joger 1986; Moody 1987; Wilms 2001; Amer & Kumazawa 2005; Wilms & Schmitz 2007).

2. MATERIAL AND METHODS

Morphological sampling and analysis

621 specimens of the genus *Uromastyx*, including the type material of the relevant taxa have been examined. The specimens are deposited in the following collections (Institutional abbreviations in parenthesis): The Natural History Museum, London (BMNH); Naturhistorisches Museum Wien (NMW); Museo Zoologico de „La Specola“, Firenze (MZUF); Muséum d’Histoire Naturelle, Genève (MHNG); Muséum National d’Histoire Naturelle, Paris (MNHN); Museum für Tierkunde, Dresden (MTKD); National Museum, Museum of Natural History Prague (NMP6V); Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt a. M. (SMF); Zoologisches Forschungsmuseum A. Koenig, Bonn (ZFMK); Zoologisches Museum der Universität Hamburg (ZMH); Museum für Naturkunde, Humbold-Universität, Berlin (ZMB) and Zoologische Staatssammlung München (ZSM). For a list of examined specimens see Appendix II.

For each specimen 25 external characters (16 meristic, 6 metric, 3 qualitative) have been routinely recorded: snout-vent length (SVL), length of tail (TL), head width between the anterior margins of the ear openings (HW), head length from the tip of the snout to the anterior margin of the ear opening on the left side (HL), width of tail between the 4th and 5th whorl (TW), maximum tail width at the 5th whorl (TW_{max}), number of tail whorls (W), number of scales beneath the 4th toe on the left side (SD), number of gular scales (from mental to a line between the anterior margins of the ear openings (G)), number of scales around mid-body (MBS), number of scales between gular- and inguinal fold (V; ventrals), number of scales around the 5th whorl (SW), number of preanofemoral pores (PP; left and right), number of enlarged scales at the anterior margin of the ear opening (LS; left and right), number of scales between suboculars and supralabials (SO; left and right), number of scales from the mid of the lower end of the ear opening to the mental scale (HS; left and right), number of scales from the upper to the lower end of the left ear opening (ES; approximately three scale rows before the anterior margin of the ear opening), number of scales from the upper end of the left ear opening to the first enlarged subocular scale (PES), presence or absence of enlarged tubercular scales at the flanks (TF; absent = 0 / present = 1), enlarged tubercular scales at the dorsum (TD; absent = 0 / present = 1 / arranged in rows = 2), intercalary scales between the whorls present or absent (IS; absent = 0 / 1–2 unkeeled present = 1 / 2–6 keeled present = 2). Measurements were taken to the nearest 0.5 mm using a calliper.

To obtain morphological outgroup data from the closest relatives of *Uromastyx* several vouchers of the genus *Leiolepis* from the collection of the ZFMK were examined.

Statistical analyses of morphological data

The Excel 2000 and SPSS (10.0) statistical packages were used to run the analyses. Hierachical Cluster analysis and Principal Component Analysis (PCA) have been selected to evaluate the morphological data and to explore the phenetic relationships between the taxa examined.

Phylogenetic analysis of morphological data

Phylogenetic analysis was carried out on the basis of twenty-five external characters (16 meristic, 6 metric, 3 qualitative). To assign a polarity to these characters (plesiomorphy vs. apomorphy), ingroup and outgroup comparisons were applied (WATROUS & WHEELER 1981; MADDISON et al. 1984). Species of the genus *Leiolepis* were used as outgroup, because this genus forms the morphologically and genetically proposed sister clade to *Uromastyx* (PETERS 1971; BÖHME 1988; SCHMITZ et al. 2001; AMER & KUMAZAWA 2005). Within the genus *Leiolepis* seven taxa are distinguished: *L. belliana* HARDWICKE & GRAY, 1827; *L. guttata* CUVIER, 1829; *L. revesii* GRAY, 1831; *L. peguensis* PETERS, 1971; *L. triploida* PETERS, 1971; *L. guentherpetersi* DAREVSKY & KUPRIYANOVA, 1993 and *L. boehmei* DAREVSKY & KUPRIYANOVA, 1993 of which three are 'agamospecies' (*L. triploida, L. guentherpetersi* and *L. boehmei*; DAREVSKY & KUPRIYANOVA 1993), which do not require fertilisation of female gametes to produce offspring.

For thirteen of the twenty-five characters polarity was unanimously assignable. These characters (ten two-state and three multistate) were defined for one outgroup (*Leiolepis*) and all twenty-three taxa in this study. A character matrix (Table 1) was designed using Nexus Data Editor (PAGE 2001) and analysed in PAUP* v4.0b10 (SWOFFORD 2002) using both neighbour-joining (NJ) and maximum parsimony (MP) algorithms. MP was run using a heuristic search and 2000 bootstrap pseudoreplicates. Detail of the character definition and coding is provided in Appendix III.

Genetic sampling

Samples of muscle tissue were taken from fresh specimens as well as from preserved specimens kept in the collection of the ZFMK, Bonn. New voucher specimens are now also kept in the herpetological collection of the ZFMK and the National Museum, Museum of Natural History Prague (NMP6V) (for a complete list of voucher specimens see Table 2).

DNA was extracted from the tissue samples using QuiAmp tissue extraction kits (Quiagen) or a modified Chelex-Protocol (WALSH et al. 1991; SCHMITZ 2003). The primers 16sar-L (light chain; 5' - CGC CTG TTT ATC AAA AAC AT - 3') and 16sbr-H (heavy chain; 5' - CCG GTC TGA ACT CAG ATC ACG T - 3') of PALUMBI et al. (1991) were used to amplify a section of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure was as described in SCHMITZ et al. (2005).

To get a better resolution within two identified clades of very closely related taxa (compare below), 12S rRNA data for representatives of those clades were added and separate trees were produced. Therefore, in these cases we amplified a section of the mitochondrial 12S ribosomal RNA gene using the primers 12SA-L (light chain; 5' - AAA CTG GGA TTA GAT ACC CCA CTA T - 3') and 12SB-H (heavy chain; 5' - GAG GGT GAC GGG CGG TGT GT - 3') of KOCHER et al. (1989). Cycling procedure was again identical as described in SCHMITZ et al. (2005).

PCR products were purified using Qiaquick purification kits (Qiagen). Sequences (including complimentary strands for assuring the accuracy of the sequences) were obtained using an automatic sequencer (ABI 377). Sequences were aligned using ClustalX (THOMPSON et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (HALL 1999). For the full dataset we performed neighbour-joining (NJ), and Bayesian reconstructions (PP), while for the two extended dataset we also calculated maximum parsimony trees. We used PAUP* 4.0b10 (SWOFFORD 2002) to compute the neighbor-joining tree, maximum parsimony tree and the uncorrected pairwise distances for all sequences. For the additional MP analysis of the combined 16S and 12S datasets, we used the heuristic search algorithm of PAUP* (SWOFFORD 2002) with 100 random additions per replicate and the TBR (tree bisection-reconnection) branch swapping option. Additionally, we used bootstrap analyses with 2000 pseudoreplicates to evaluate the relative branch support in the phylogenetic analysis. For the Bayesian analysis parameters of the model were estimated from the data set using MrModeltest 2.2 (NYLANDER 2004) and the analyses were performed with MrBayes, version 3.0b4 (HUELSENBECK & RONQUIST 2001). The comparison between the different likelihood scores for each model showed that the GTR + Γ model (YANG 1994) was determined to be the optimal model for the data set. For the Bayesian analyses we ran two MCMC analyses for 10^6 generations each. The initial 100000 (10%) trees were disregarded as "burn-in". We consider probabilities of 95 % or greater to be significantly supported. The exact parameters used for the Bayesian analyses followed those described in detail by REEDER (2003).

Sixty-four 16S sequences comprising 555 bp (lengths referring to the aligned sequences including gaps) as well as thirty-two 12S sequences comprising 434 bp were obtained. Sequences have been submitted to GenBank; for accession numbers see Tab. 2. *Tympanocryptis tetraporophora* Lucas & Frost, 1895 (Agamidae: Amphibolurinae), *Agama impalearis* Boettger, 1874 (Agamidae: Agaminae), *A. planiceps* Peters, 1862 (Agamidae: Agaminae), *Leiolepis b. belliana* Hardwicke & Gray, 1827 (Agamidae, Leiolepidinae), *L. r. reevesii* Gray, 1831

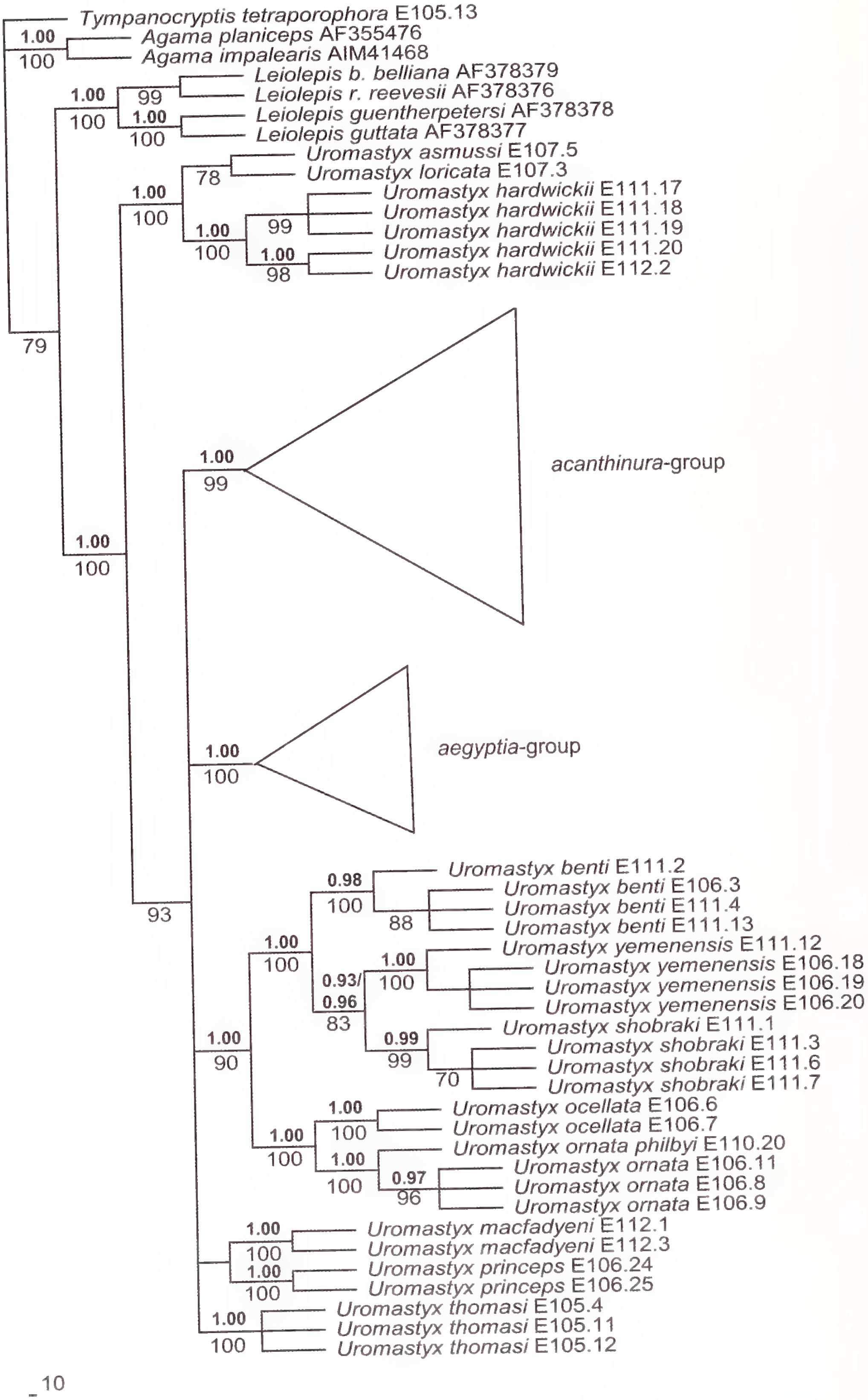
Tympanocryptis tetraporophora E105.13
Agama planiceps AF355476
Agama impalearis AIM41468
Leiolepis b. belliana AF378379
Leiolepis r. reevesii AF378376
Leiolepis guentherpetersi AF378378
Leiolepis guttata AF378377
Uromastyx asmussi E107.5
Uromastyx loricata E107.3
Uromastyx hardwickii E111.17
Uromastyx hardwickii E111.18
Uromastyx hardwickii E111.19
Uromastyx hardwickii E111.20
Uromastyx hardwickii E112.2
acanthinura-group
aegyptia-group
Uromastyx benti E111.2
Uromastyx benti E106.3
Uromastyx benti E111.4
Uromastyx benti E111.13
Uromastyx yemenensis E111.12
Uromastyx yemenensis E106.18
Uromastyx yemenensis E106.19
Uromastyx yemenensis E106.20
Uromastyx shobraki E111.1
Uromastyx shobraki E111.3
Uromastyx shobraki E111.6
Uromastyx shobraki E111.7
Uromastyx ocellata E106.6
Uromastyx ocellata E106.7
Uromastyx ornata philbyi E110.20
Uromastyx ornata E106.11
Uromastyx ornata E106.8
Uromastyx ornata E106.9
Uromastyx macfadyeni E112.1
Uromastyx macfadyeni E112.3
Uromastyx princeps E106.24
Uromastyx princeps E106.25
Uromastyx thomasi E105.4
Uromastyx thomasi E105.11
Uromastyx thomasi E105.12
1.00
100
1.00
99
100
1.00
100
78
1.00
100
1.00
99
100
1.00
98
79
1.00
99
1.00
100
1.00
100
93
0.98
100
88
1.00
100
1.00
0.93/
100
0.96
83
0.99
99
70
1.00
90
1.00
1.00
100
100
1.00
100
0.97
96
1.00
100
1.00
100
1.00
100
10

Fig. 1. Cladogram of the tree recovered by the analyses based on 555 bp of the 16S mitochondrial RNA gene. Upper (bold) values at the nodes are Bayesian posterior probabilities (values below 0.5 not shown); lower values are neighbor-joining bootstrap replicates (values below 50 % not shown).

(Agamidae, Leiolepidinae), *L. guentherpetersi* Darevsky & Kupriyanova, 1993 (Agamidae, Leiolepidinae) and *L. guttata* Cuvier, 1829 (Agamidae, Leiolepidinae) were used as outgroup. 16S Sequences for all species used as outgroup, with the exception of *T. tetraporophora*, have been obtained vom GenBank.

3. RESULTS

Results of the phylogenetic analysis of genetic data

Uromastyx sensu lato and *Leiolepis* group together in a large clade supported by a neighbour joining bootstrap value of 79 (Fig. 1) and is the sister group to a clade including *Agama planiceps* and *A. impalearis*. Within this clade *Leiolepis* and the ingroup are separated in fully supported subclades (PP: 1.00 / NJ: 100 for *Leiolepis*; PP: 1.00 / NJ: 100 for *Uromastyx* sensu lato). The ingroup itself forms again two well separated clades: in the first one *U. hardwickii* groups with the sister species *U. asmussi* and *U. loricata*, while in the second all other taxa of the genus *Uromastyx* are present (*Uromastyx* sensu stricto). Both clades are supported at least by very high and significant NJ bootstrap values (*U. hardwickii, U. asmussi, U. loricata* clade: PP: 1.00 / NJ: 100; *Uromastyx* s. s.: PP: <0.95 / NJ: 93).

Genetic distances (uncorrected p-distances, 16S rRNA gene) from *U. hardwickii*, *U. asmussi* and *U. loricata* to all other taxa are as follows: *hardwickii*: 10.2–14.2 %, *asmussi*: 8.6–13.0 %, *loricata*: 8.2–12.1 %.

Within *Uromastyx* sensu stricto five well supported clades are recognizable but the direct relationships of these clades are not resolved, as they are forming an unresolved polytomy.

Uromastyx hardwickii, U. asmussi and *U. loricata* clade

The clade including these three afore mentioned species shows a substructure with two principal subclades. Beside the clade consisting of the sister taxa *U. asmussi* and *U. loricata* (NJ: 78), a second well supported clade (PP: 1.00 / NJ: 100) comprising all five *U. hardwickii*-specimens. This latter clade also shows another clear separation with taxa-units of three and two *hardwickii*-specimens respectively and both these terminal clades are significantly supported by at least one bootstrap value (ZFMK 83794, 83795, 83797: NJ: 99; ZFMK 83796, sample without voucher specimen: PP: 1.00 / NJ: 98). We preliminarily assigned the second subcluster exclusively to *Uromastyx hardwickii*, but data suggest that in fact two taxa may be involved (see also discussion).

Genetic distances between the taxa of the *Uromastyx hardwickii, U. asmussi* and *U. loricata* clade are as follows: *asmussi-loricata*: 2.9 %; *asmussi-hardwickii*: 5.8–6.5 %; *loricata-hardwickii*: 6.1–6.7. Distance between the two identified subclades within *hardwickii* is rather low at 0.9 %.

Uromastyx sensu stricto clade

Based on the genetic data four of the five clearly recognizable clades are strongly supported by bootstrap values: *Uromastyx acanthinura* group (PP: 1.00 / NJ: 99); *U. aegyptia* group (PP: 1.00 / NJ: 100); *U. ocellata* group (PP: 1.00 / NJ: 90) and *U. thomasi* (PP: 1.00 / NJ: 100). The fifth clade comprising *U. macfadyeni* and *U. princeps* is only very weakly supported. To get a better resolution within the *U. acanthinura* and the *U. aegyptia* clades 12S rRNA data were added and separate trees were produced.

Uromastyx acanthinura group

Based on the genetic data the *U. acanthinura* clade (Fig. 1), including the taxa *geyri*, *acanthinura*, *nigriventris*, *dispar*, *flavifasciata* and *maliensis* (*alfredschmidti* was not included in this analysis due to the non-availability of DNA samples), is very well supported by bootstrap values (PP: 1.00 / NJ: 99). Intraspecific genetic distances within all taxa of the *U. acanthinura* group was 0.0–0.4 % (exception *U. geyri*: 0.9 %). Between the taxa of this group, genetic distances are 0.2–1.4 %. On the basis of these data, decisions on the rank of the taxa in question were not possible. To further enhance the resolution of the tree, 12S rRNA data were combined with the 16S rRNA data and new trees were produced using *U. ornata* as outgroup (Fig. 2). The newly calculated tree shows the *geyri* clade basal to all other taxa within the *U. acanthinura* group. This clade is maximally supported (PP: 1.00 / NJ: 100 / MP: 100) and forms the sister taxon to all other members of the *U. acanthinura* group, which form a clade significantly supported by bootstrap values (NJ: 88 / MP: 100). This clade shows a very well supported substructure with *nigriventris* being the sister taxon (PP: 1.00 / MP: NJ: 100 / MP: 100) of the clade including *acanthinura* and *U. dispar* spp. On the basis of this tree, *acanthinura* is the sister taxon to the clade comprising the taxa *dispar*, *flavifasciata* and *maliensis* with both clades being significantly supported by at least NJ and MP bootstrap values (*acanthinura* clade: PP: 0.97/0.95 / NJ: 100 / MP: 100; *dispar* clade: PP: 0.75/0.80 NJ: 85 / MP: 90). As it was not possible to win a 12S DNA-sequence from the only available representative of *maliensis* and we still wanted to include all described taxa in our analyses, we filled the missing 12S sequence information with "N"s and calculated the phylogenetic trees both with and without the inclusion of *maliensis*. This was done to check if the inclusion of the

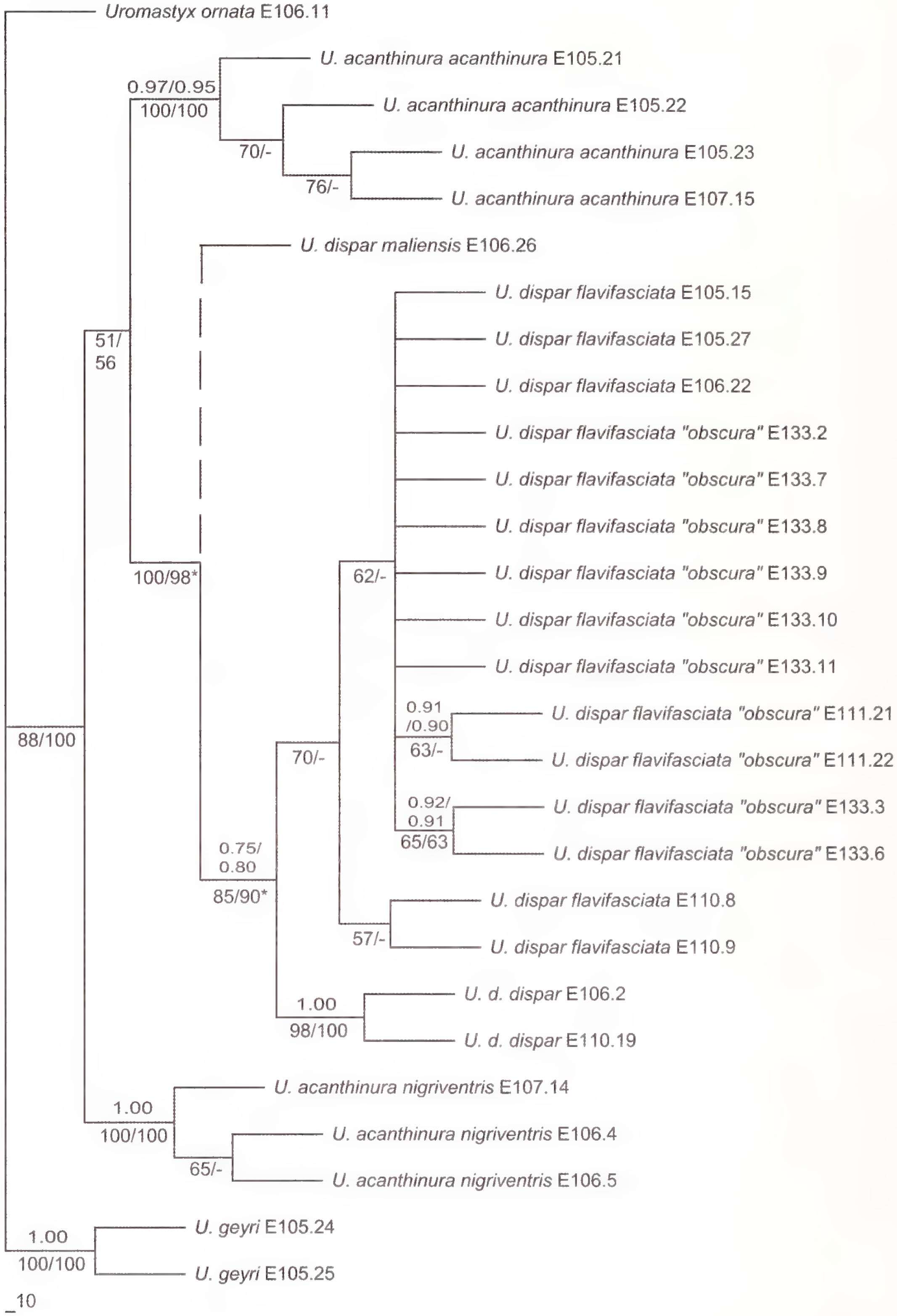
Uromastyx ornata E106.11
U. acanthinura acanthinura E105.21
U. acanthinura acanthinura E105.22
U. acanthinura acanthinura E105.23
U. acanthinura acanthinura E107.15
U. dispar maliensis E106.26
U. dispar flavifasciata E105.15
U. dispar flavifasciata E105.27
U. dispar flavifasciata E106.22
U. dispar flavifasciata "obscura" E133.2
U. dispar flavifasciata "obscura" E133.7
U. dispar flavifasciata "obscura" E133.8
U. dispar flavifasciata "obscura" E133.9
U. dispar flavifasciata "obscura" E133.10
U. dispar flavifasciata "obscura" E133.11
U. dispar flavifasciata "obscura" E111.21
U. dispar flavifasciata "obscura" E111.22
U. dispar flavifasciata "obscura" E133.3
U. dispar flavifasciata "obscura" E133.6
U. dispar flavifasciata E110.8
U. dispar flavifasciata E110.9
U. d. dispar E106.2
U. d. dispar E110.19
U. acanthinura nigriventris E107.14
U. acanthinura nigriventris E106.4
U. acanthinura nigriventris E106.5
U. geyri E105.24
U. geyri E105.25
0.97/0.95
100/100
70/-
76/-
51/
56
100/98*
62/-
0.91
/0.90
63/-
88/100
70/-
0.92/
0.91
65/63
0.75/
0.80
85/90*
57/-
1.00
98/100
1.00
100/100
65/-
1.00
100/100
10

Fig. 2. Cladogram of the tree recovered by the analyses based on 989 bp of the combined 16S and 12S mitochondrial RNA genes. Upper values at the nodes are Bayesian posterior probabilities (values below 0.5 not shown); lower values on the right are maximum-parsimony bootstrap replicates; lower values on the left are neighbor-joining bootstrap replicates (values below 50 % not shown). The line connecting to *Uromastyx dispar maliensis* is dotted to incorporate the fact that we were not able to get a 12S sequence for this species and that we had to fill up the alignment with "N"s to include the species in the calculation.

incomplete sequence would alter the tree topologies. As this was not the case, we added the sequence and have marked its calculated position with a broken line.

Within the *dispar* clade three fairly well supported subunits are recognizable (for exact bootstrap values see Fig. 2), corresponding to the currently valid subspecies *dispar*, *flavifasciata* and *maliensis*, while the recently described "*obscura*"-form is included in and identical (no genetic difference) with *flavifasciata*.

Intraspecific genetic distances within the terminal taxa (lumping data for the subspecies of *U. dispar*) are: *acanthinura*: 0.0-0.1%, *nigriventris*: 0.0–0.1%, *geyri*: 0.4%, *dispar*: 0.0–0.7%. Distances between the taxa are: *acanthinura-geyri*: 4.57–4.69 %, *nigriventris-geyri*: 4.46–4.57 %, *dispar-geyri*: 4.21–4.99 %, *acanthinura-nigriventris*: 2.0–2.3 %, *acanthinura-dispar*: 1.54–2.44 %, *nigriventris-dispar*: 1.72–3.08 %.

Uromastyx aegyptia group

The calculation for the extended dataset for the taxa of the *U. aegyptia*-group produced an identical topology (tree not shown) for all three algorithms, with the following structure [numbers are bootstrap values (PP/NJ/MP) for the following nodes; significant values in bold; values below 0.90 (PP) or under 50 (NJ/MP) (*) not shown]:

(*Uromastyx ornata*), */**100** (*Uromastyx a aegyptia*, */59/55 (*Uromastyx a. microlepis*, 0.94/55/52 (*Uromastyx a. microlepis*, **1.00**/93/94 (*Uromastyx leptieni*, *Uromastyx leptieni*))))

Within taxa genetic distances are extremely low: *microlepis*: 0.10 %, *leptieni*: 0.13 % (for *aegyptia* only a single specimen was sequenced), while between the different taxa genetic difference were comparatively much higher: *aegyptia-microlepis*: 0.3–0.4 %, *microlepis-leptieni*: 0.3–0.6 %, *aegyptia-leptieni*: 0.7–0.9 %.

Uromastyx ocellata group

The *Uromastyx ocellata* group constitutes a further well supported clade (Fig. 1) which is itself again subdivided: the first main clade comprises the taxa *ornata* (including the single specimen of *philbyi*) and *ocellata* (PP: 1.00 / NJ: 100). Both of the nominal taxa are clearly separate species-units (PP: 1.00 / NJ: 100).

The second clade comprises a well supported substructure, consisting of three subclades which correspond to the taxa *benti*, *yemenensis* and *shobraki* (PP: 1.00 / NJ: 90). Each of these taxa is fully supported (*benti*: PP: 0.98 / NJ: 100; *yemenensis*: PP: 1.00 NJ: 100; *shobraki*: PP: 0.99 / NJ: 99).

Intraspecific genetic difference is very low: *benti*: 0.0–0.4 %, *yemenensis*: 0.0–0.2, *shobraki*: 0.0–0.2, *ocellata*: 0.2 %, *ornata* (without *philbyi*): 0.0 %. As expected, the interspecific genetic distances are much higher: *benti-yemenensis*: 2.2–2.7 %, *benti-shobraki*: 2.2–2.9 %, *yemenensis-shobraki*: 1.8–2.0 %, *benti-ocellata*: 6.5–7.2 %, *benti-ornata*: 5.8–6.3 %, *yemenensis-ocellata*: 7.2–7.4 %, *yemenensis-ornata*: 6.5 %, *shobraki-ocellata*: 7.0–7.4 %, *shobraki-ornata*: 6.5–7.0 %, *ocellata-ornata* (including *philbyi*): 3.6–4.0 %. Genetic difference between *ornata* and *philbyi* is 0.7 %.

Uromastyx macfadyeni / *Uromastyx princeps* clade

This is the only major clade (Fig. 1) which is not significantly supported on its basal node; it therefore comprises two clearly separated species units (each with PP: 1.00 / NJ: 100), whose direct relationships remain unclear. Intraspecific genetic difference is: *macfadyeni*: 0.0 %, *princeps*: 0.2 %. Between those two taxa, the genetic difference is 9.0–9.5%.

Uromastyx thomasi clade

Uromastyx thomasi forms a separate, well supported clade of its own (PP: 1.00 / NJ: 100).

Intraspecific genetic difference is 0.2–0.3 %.

Results of the multivariate analyses of the taxa of the genus *Uromastyx*

A distance phenogram based on the average values of 18 characters for all taxa of the genus *Uromastyx* (number of taxa = 22; *Uromastyx occidentalis* data were not available; for definition of variables see Table 3) was calculated using the complete linkage method (Fig. 3). The resulting distance phaenogram shows two distinct main clusters (OTU I & OTU II), of which one includes *hardwickii*, *loricata* and *asmussi* (OTU II), while the second cluster represents all remaining taxa of the genus (OTU I). Within this second cluster five subcluster based on phenetic similarity are recognizable – the first cluster contains *aegyptia*, *microlepis* and *leptieni*; the second *ocellata*, *yemenensis*, *shobraki* and *benti*, the third *dispar*, *maliensis*, *flavifasciata*, *acanthinura* and *nigriventris*; the fourth *princeps* and the fifth clade contains *alfredschmidti*, *geyri*, *thomasi*, *macfadyeni*, *ornata* and *philbyi*.

Because of these morphological findings based on average values, we suggest, that the genus *Uromastyx* s.l. consist of two clades which are different. To further evaluate the phenetic relationships within the genus we applied a principal component analysis (PCA) on data obtained from 481 individuals (Variables: V1–V17; see Table 4). The dis-

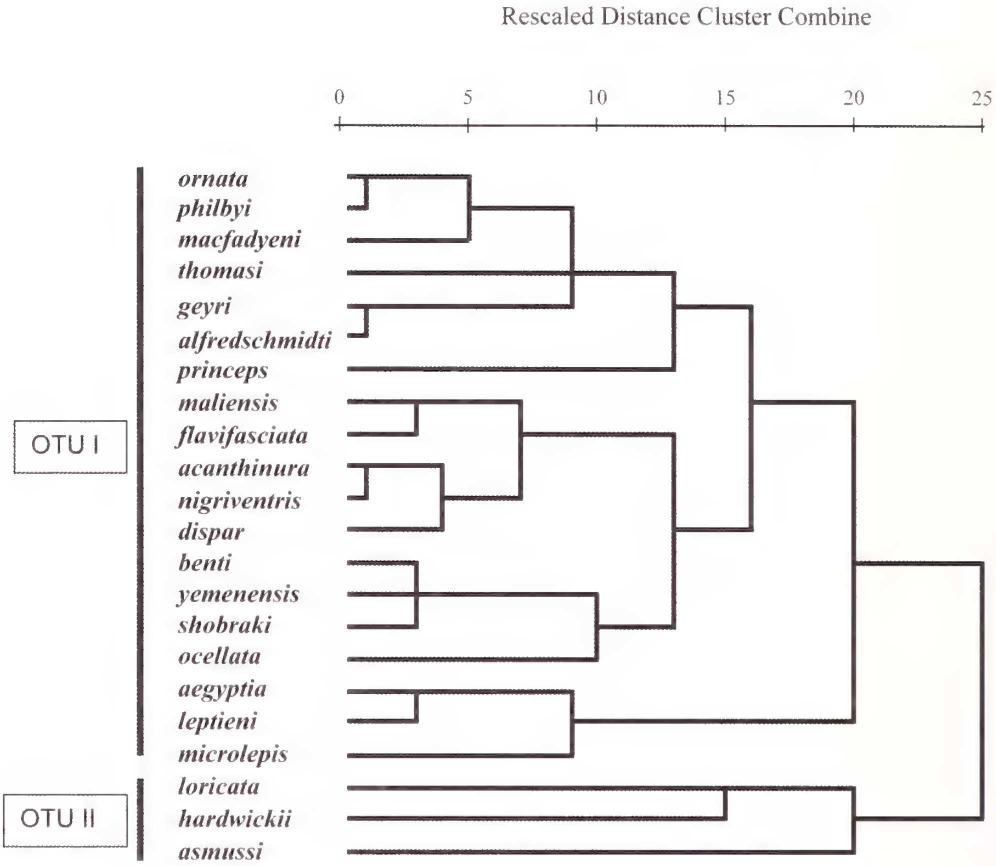
Rescaled Distance Cluster Combine
0
5
10
15
20
25
OTU I
OTU II
ornata
philbyi
macfadyeni
thomasi
geyri
alfredschmidti
princeps
maliensis
flavifasciata
acanthinura
nigriventris
dispar
benti
yemenensis
shobraki
ocellata
aegyptia
leptieni
microlepis
loricata
hardwickii
asmussi

Fig. 3. Distance phenogram resulting from cluster analysis of average values of Variable V1–V18 (see Tab. 4) of the taxa of *Uromastyx* sensu lato (Hierarchical cluster using complete linkage, Tschebyscheff distances and z-transformation).

crepancy between the total number of specimens used in this study and the number of specimens subject to the statistical analysis is because of the elimination of incomplete datasets.

In the projection of the first two principal components all specimens of *hardwickii* cluster seperately as well as all specimens of *asmussi* and *loricata* respectively. Both clusters are clearly separated from all specimens of the remaining *Uromastyx* taxa (Fig. 4; for factor loadings on principal components see Table 5), and correspond to the clusters identified as OTU I and OTU II in the hierarchical cluster. OTU II contains two clearly separated subclusters with all *U. hardwickii* clustering together as well as *U. asmussi* and *U. loricata*. The finding of two phenetic clusters clearly outside the *Uromastyx* sensu stricto cluster as well as the identification of two well supported genetic clades raise the question of a polyphyletic origin of the genus *Uromastyx* sensu lato.

To evaluate the phenetic relationships and to discriminate the species or species groups within *Uromastyx* sensu stricto, data of all taxa (without *U. occidentalis*) were subject of six PCAs (Variables: V1–V15; see Table 6). Between the subsequent PCAs, data of taxa clustering outside the respective main clusters were removed. As a result of this procedure seven entities containing single species or phenetically similar taxa were recovered:

1. *benti*, *yemenensis*, *shobraki*, *princeps* (Fig. 5; for factor loadings on principal components see Table 7)

2. *ocellata* (Fig. 6; for factor loadings on principal components see Table 8)

3. *thomasi* (Fig. 7; for factor loadings on principal components see Table 9)

4. *aegyptia, microlepis, leptieni* (Fig. 8; for factor loadings on principal components see Table 10)

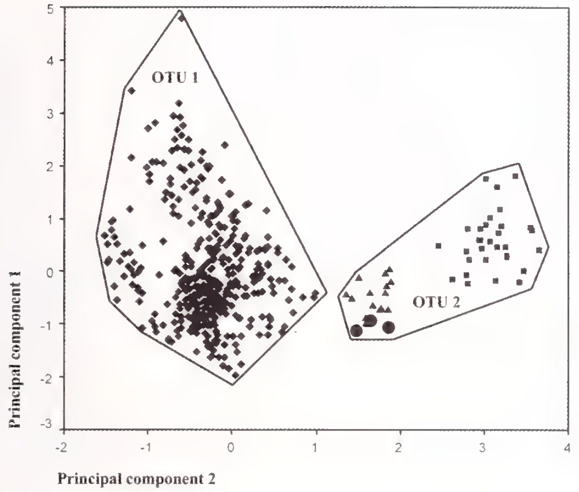

Fig. 4. Projection of the first two principal components from a PCA run on 481 individuals assignable to OTU 1 and OTU 2 (◆ = *Uromastyx* sensu stricto; ▲ = *Uromastyx loricata*;) ● = *Uromastyx asmussi*; ■ = *Uromastyx hardwickii*).

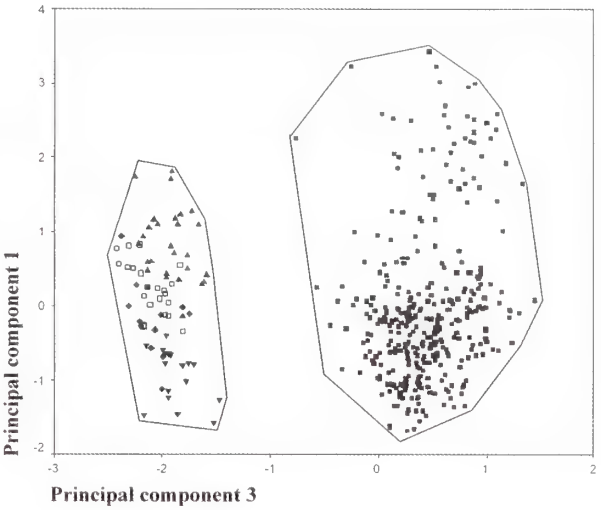

Fig. 5. Projection of the first and third principal component from a PCA run on 431 individuals assigned to *Uromastyx* sensu stricto (OTU 1) (◆ = *Uromastyx yemenensis*, ▲ = *Uromastyx princeps*; ▼ = *Uromastyx benti*; □ = *Uromastyx shobraki*; ■ = *Uromastyx* spp.).

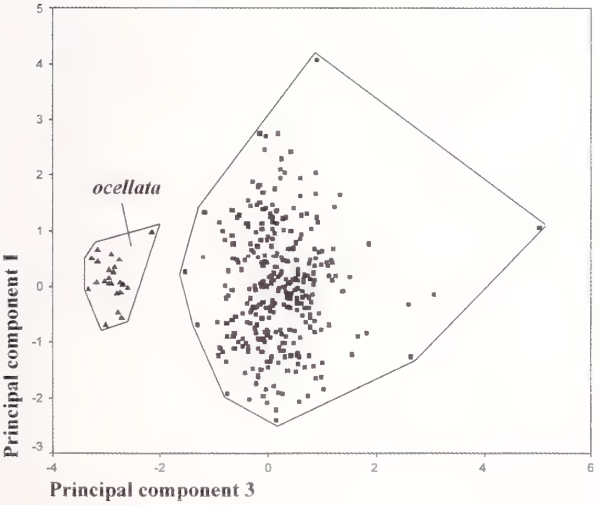

Fig. 6. Projection of the first and third principal component from a PCA run on 354 individuals assigned to *Uromastyx* sensu strico without *yemenensis*, *benti*, *shobraki* and *princeps* (■ = *Uromastyx* spp., ▲ = *Uromastyx ocellata*).

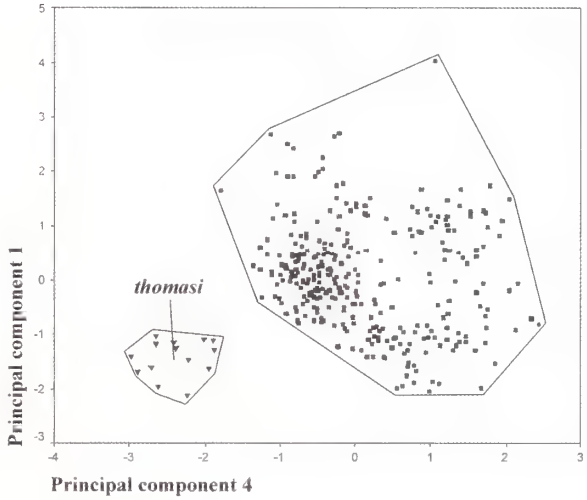

Fig. 7. Projection of the first and fourth principal component from a PCA run on 331 individuals assigned to *Uromastyx* sensu strico without *yemenensis*, *benti*, *shobraki*, *princeps* and *ocellata* (■ = *Uromastyx* spp.; ▼ = *Uromastyx thomasi*).

5. *dispar, flavifasciata, maliensis* (Fig. 9; for factor loadings on principal components see Table 11)
6. *acanthinura, nigriventris* (Fig. 10; for factor loadings on principal components see Table 12)
7. *alfredschmidti, geyri, ornata, philbyi, macfadyeni* (Fig. 10)

These seven clusters are based on external similarities and therefore do not exclusively reflect phylogenetic relationships but also identify phenetic similarities based on homoplasious character states. To evaluate phenetic relationships within the clades identified by genetic analysis, separate PCAs were applied to the data sets of the taxa.

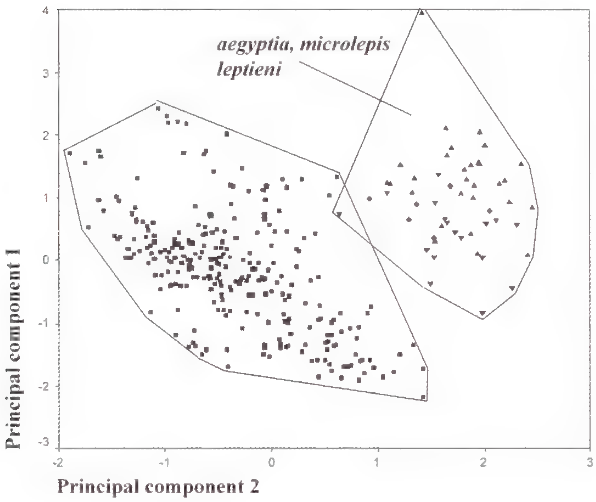

Fig. 8. Projection of the first two principal components from a PCA run on 317 individuals assigned to *Uromastyx* sensu stricto without *yemenensis*, *benti*, *shobraki*, *princeps*, *ocellata* and *thomasi* (■ = *Uromastyx* spp., ▲ = *Uromastyx a. microlepis*; ▼ = *Uromastyx a. aegyptia*; ◆ = *Uromastyx a. leptieni*).

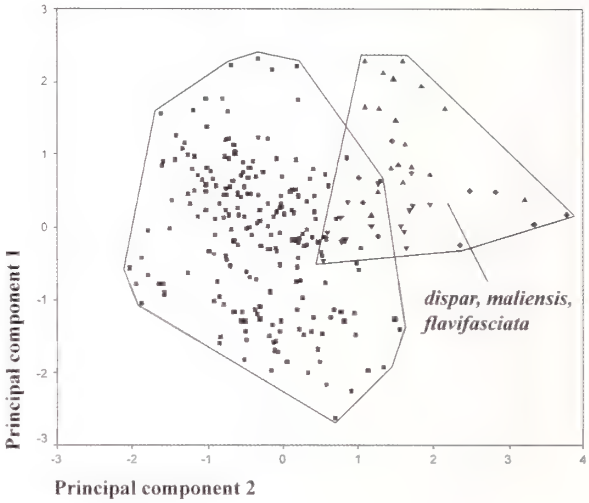

Fig. 9. Projection of the first two principal components from a PCA run on 265 individuals assigned to *Uromastyx* sensu stricto without *yemenensis*, *benti*, *shobraki*, *princeps*, *ocellata*, *thomasi*, *aegyptia*, *microlepis* and *leptieni* (■ = *Uromastyx* spp., ▲ = *Uromastyx dispar maliensis*; ◆ = *Uromastyx d. flavifasciata*; ▼ = *Uromastyx d. dispar*).

Uromastyx acanthinura group

The taxa of the *U. acanthinura* group cluster in three subsequent PCAs (PCA 5, 6 & 7). This indicates, that the morphology of the taxa of this group is to some degree different to the other species of the genus (see also discussion regarding cluster 7 also containing taxa not belonging to the *U. acanthinura* group).

PCAs carried out exclusively on the data of the *U. acanthinura* group revealed, that *U. geyri* and *U. alfredschmidti* cluster outside of the remaining taxa. Separation of *acanthinura*, *nigriventris*, *dispar*, *flavifasciata* and *maliensis* by means of PCA was not possible (data not shown; Variables: V1–V15).

Uromastyx aegyptia group

All taxa in this study belonging to this group cluster in one single PCA (PCA 4). Phenetical relationships within the taxa of the *U. aegyptia* group (excluding *U. occidentalis*) have already been assessed by WILMS & BÖHME (2007). Analysis revealed that male specimens could be assigned according to the a priori specimen classification using cluster analysis and PCA. For females taxon discrimination was not possible.

Uromastyx ocellata group

The taxa of the *U. ocellata* group are included in several clusters of the previous PCAs (PCA 1, 2 & 7). This indicates, that some taxa of this group are readily distinguishable from other taxa of the genus (see also discussion regarding cluster 1 & 7 containing not only taxa belonging to the *U. ocellata* group).

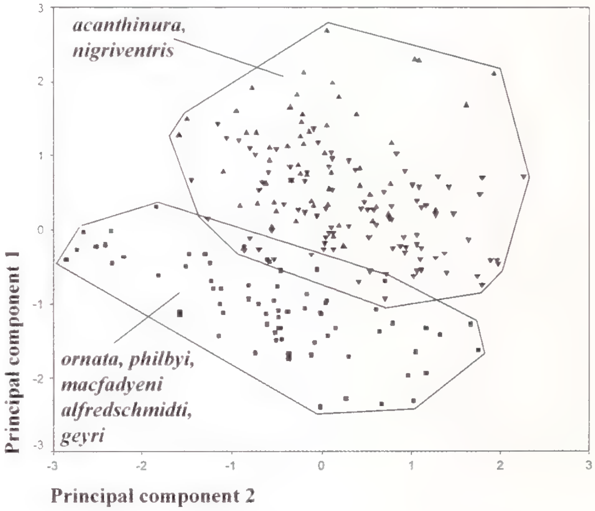

Fig. 10. Projection of the first two principal components from a PCA run on 223 individuals assigned to *Uromastyx* sensu stricto without *yemenensis*, *benti*, *shobraki*, *princeps*, *ocellata*, *thomasi*, *aegyptia*, *microlepis*, *leptieni*, *maliensis*, *dispar* and *flavifasciata* (■ = *Uromastyx* spp., ▲ = *Uromastyx acanthinura*; ▼ = *Uromastyx nigriventris*).

A PCA carried out only on data of the specimens belonging to the *U. ocellata* group (data not shown) revealed, that two taxa cluster completely separate (*ocellata*, *benti*) while *shobraki* and *yemenensis* form a common cluster as well as *ornata* and *philbyi* (Variables: V1–V15).

Uromastyx macfadyeni / *Uromastyx princeps* clades

Both species cluster in different PCAs (No. 1 & 7) and are clearly separated in the PCA carried out solely on data of both species (data not shown; variables: V1–V15).

Uromastyx thomasi group

U. thomasi already clustered completely separate in one of the subsequent PCAs applied to data of the whole genus (PCA 3).

Results of the phylogenetic analysis of morphological data

A NJ analysis was carried out (tree not shown) and a MP heuristic parsimony analysis resulted in 254 shortest trees (L: 254, CI: 0.762, RI: 0.857, RC: 0.653) (not shown) whose 50% majority-rule consensus shows the following structure [numbers are bootstrap values (NJ/MP) for the following nodes; significant values in bold; values under 50 not shown *]:

(((((*acanthinura*,(((*aegyptia*, *microlepis*)**70**/56, *leptieni*)61/64, *occidentalis*)56/64, *alfredschmidti*,(*benti*, *macfadyeni*, *ocellata*,(*ornata*, *philbyi*)55/*, *shobraki*, *yemenensis*)53/**71**, *dispar*, *flavifasciata*, *geyri*, *maliensis*, *nigriventris*)56/*,(*princeps*, *thomasi*)**100**/**98**)**70**/**71**,(*asmussi*, *loricata*)**94**/*)53/*, *hardwickii*)**100**/**100**, *Leiolepis*)

Even though the resolution of the phylogenetic analysis of the morphological data is not surprisingly rather limited, the node separating *Leiolepis* from *Uromastyx* sensu lato is fully supported by bootstrap values (**100**/**100**), and more importantly the node separating *Uromastyx* sensu stricto from *U. hardwickii*, *U. loricata* and *U. asmussi* is also well supported in both analyses (**70**/**71**).

Synthesis and discussion of the morphological and genetic results

As pointed out by Amer & Kumazawa (2005) the relationship between *Leiolepis* and *Uromastyx* has been subject to scientific discussions. Based on morphology both genera possess autapomorphies supporting the monophyly of this clade within the Acrodontia and their position as the sister taxon to all remaining agamids (Moody 1980; Böhme 1982). Studies based on molecular data sets failed to support this monophyly (Macey et al. 1997, 2000) or did not place this clade as the sister taxon of the remaining agamids (Honda et al. 2000). We used members of the Agaminae (*Agama planiceps*, *A. impalearis*) and Amphibolurinae (*Tympanocryptis tetraporophora*) as outgroups in our analysis and found a weakly supported monophyly of the clade consisting of *Leiolepis* and *Uromastyx*. This result is consistent with the phylogeny established by Amer & Kumazawa (2005) also based on mtDNA.

Ananjeva et al. (2004, 2007) integrated morphological and molecular data and established a classification of agamid lizards by distinguishing six monophyletic lineages on subfamily level: Uromastycinae Theobald, 1868; Leiolepidinae Fitzinger, 1843; Amphibolurinae Wagler, 1830; Hydrosaurinae Kaup, 1828; Draconinae Fitzinger, 1826; Agaminae Spix, 1825. We follow this concept of Ananjeva et al. and regard the Leiolepidinae and Uromastycinae as separate lineages.

Our observations based on morphological and genetic data show a clear and well supported substructure within *Uromastyx* s.l. Both of these entities warrant recognition on genus level. For the clade comprising the taxa of the irano-turanian subregion (*hardwickii*, *asmussi*, *loricata*) the genus name *Saara* Gray, 1845 is available. We therefore resurrect *Saara* as the sister genus of *Uromastyx*. After the resurrection of the genus *Saara* for the species of the irano-turanian region, two genera are now placed within the Uromastycinae: *Saara* and *Uromastyx*. After the exclusion of the species of the genus *Saara*, *Uromastyx* is now monophyletic comprising 20 nominal taxa.

An early separation of *hardwickii* from the other species of the genus *Uromastyx* was already proposed by Joger (1986) based on immunological distances and Amer & Kumazawa (2005) based on molecular data. Joger (1986) furthermore established a close phylogenetic relationship between *hardwickii* and *loricata*. This author suggested that *Uromastyx* should be divided into several subgenera (one of them being the clade of *hardwickii* and *loricata*), but did not impose formal taxonomic changes with the exception of the resurrection of the name *Aporoscelis* for the two broad tailed species (*U. thomasi* and *U. princeps*). As Moody (1987) pointed out, applying this concept would have caused the genus *Uromastyx* to be paraphyletic. The separation between *Saara hardwickii* and the species of the Afro-Arabian radiation of *Uromastyx* was estimated at 25–29 Mya (Amer & Kumazawa 2005) which is in general accordance with the estimates made by Joger (1986). Within *Saara* a clear substructure is recognizable with *S. asmussi* and *S. loricata* forming sister clades which are themselves the sister taxa to *S. hardwickii*.

The situation and relationships within *Uromastyx* are not as clear as in *Saara*. Genetically, we recognize five species groups within the genus of which four are at least partly supported by morphological data (*U. acanthinura* group, *U. aegyptia* group, *U. ocellata* group, *U. thomasi* group). The remaining group (cluster containing *U. princeps* and *U. macfadyeni*), feebly recognized on the basis of the molecular data set, is not supported by morphological data.

Differences in the composition of genetically based clusters and morphologically based groups might mainly be the result of a convergent evolution of the taxa involved due to similar ecological or climatic environments.

Well supported by morphological analysis are the *U. aegyptia* and the *U. thomasi* groups. While *U. thomasi* clusters completely separate in the PCA analysis, all taxa of the *U. aegyptia* group cluster together according to the genetic results (hierarchical cluster, PCA analysis, PAUP analysis of morphological data). It is therefore well established, that *U. thomasi* and the *U. aegyptia* group form phylogenetic entities of their own. This is especially remarkable for *U. thomasi*, because this species has in former studies been placed in a clade together with *U. princeps* (JOGER 1986; MOODY 1987; WILMS 2001) with which it also clusters in the PAUP analysis of morphological data (this study). The present study is the first including DNA samples of both broad tailed *Uromastyx* species and therefore recovers a biased morphological interpretation in the phylogenetic relationship of these two taxa. The overall similarity between *U. thomasi* and *U. princeps* is most possibly based on the extraordinary short tail in those taxa which was misinterpreted as an autapomorphy for this group instead of an independantly evolved analogous character state. From our point of view the phylogenetic affiliation of *U. princeps* and *U. macfadyeni* is probable, though this is not conclusive due to the low bootstrap values (PP: 0.77 / NJ: 51). AMER & KUMAZAWA (2005) found a sister group relationship of *U. macfadyeni* with species of the *U. acanthinura* clade (*U. geyri*, *U. acanthinura*, *U. dispar*), which we cannot confirm based on our own data. Nevertheless the relationships within the *U. acanthinura* group in this previous (AMER & KUMAZAWA 2005) and in the present study are in good accordance.

Within the North African *Uromastyx acanthinura* group seven taxa are recognized, of which all but *U. alfredschmidti* were available for genetic analysis. Based on 12S and 16S rRNA data *geyri* is the sister taxon of the clade comprising *acanthinura*, *nigriventris* and *U. dispar* ssp. As reported earlier *nigriventris* is the sister taxon of the two remaining taxa, which form themselves strongly supported clades.

Morphologically *acanthinura* and *nigriventris* as well as *dispar*, *flavifasciata* and *maliensis* form clusters in subsequent PCA analysis. These taxa cluster in the 5th and 6th PCA cycle respectively. All specimens of *geyri* and *alfredschmidti* remained in a cluster together with *ornata*, *philbyi* and *macfadyeni*, for which a further resolution was not possible based on the PCA methodology. It is evident, that the assingnment of *geyri* and *alfredschmidti* to the three taxa mentioned above is because of a superficial morphological similarity within the taxa in question, which is due to similar ecological adaptations (convergent evolution) and not due to phylogenetic relationships (all of them are predominantly rock dwelling species).

Another PCA was carried out exclusively on specimens belonging to the taxa of the *U. acanthinura* clade. In this PCA *geyri* and *alfredschmidti* clustered together and outside of the remaining taxa, with only a very small area of overlap between the respective clusters (data not shown). It was not possible to separate the remaining taxa with a further PCA.

On the basis of the morphological data we consider *dispar*, *flavifasciata* and *maliensis* as being closely related entities, as well as *geyri* and *alfredschmidti*. The taxa *acanthinura* and *nigriventris* show a certain morphological similarity, which led in the past to the conclusion to tread both taxa as subspecies of a single species (WILMS & BÖHME 2001).

We suppose, that the *U. acanthinura* clade in North Africa represents a relatively recent radiation within the genus (see also WILMS 2001). This hypothesis is supported by the relatively low level of genetic difference within all taxa of this group, which is generally between 0.0 and 1.4 % difference in the 16S rRNA gene (within *Uromastyx*, only one further group shows a similarily low degree of separation: the *U. aegyptia* group) as well as the overall similarity concerning scalation characters. By including data for the 12S rRNA gene the resolution of taxa discrimination was significantly enhanced, resulting in genetic distances suitable to distinguish between the taxa involved. As has been shown earlier in this study, *acanthinura* as well as *nigriventris* exhibit a very low intraspecific genetic distance of 0.0–0.1 %, while *dispar* shows a respective distance up to 0.7 %. We have therefore assessed the internal distances within the nominal taxa *dispar*, *flavifasciata* and *maliensis*, which proved to be: *dispar* 0.0 %, *flavifasciata* 0.0–0.2 % and *maliensis* 0.0 (only one sequence available). The respective distances between those taxa are: *dispar-flavifaciata*: 0.53–0.74 %, *dispar-maliensis*: 0.58 %, *maliensis-flavifasciata*: 0.39–0.58 %. We therefore recognize *dispar*, *flavifasciata* and *maliensis* as valid taxa belonging to one species, *Uromastyx dispar*, but being differentated on subspecific level.

To evaluate a further taxonomic problem, we have included several melanistic specimens of *flavifasciata* from northern Mauritania in this study. These animals have been described as *Uromastyx flavifasciata obscura* by MATEO et al. (1998), and the validity of this taxon was under debate ever since (WILMS & BÖHME 2001; GENIEZ et al. 2004). The genetic difference between these animals and typical *U. dispar flavifasciata* is 0.0–0.2 %. We therefore consider *obscura* to be synonymous with *flavifasciata* (see also WILMS & BÖHME 2001).

As a synthesis of our morphological and molecular data we consider five evolutionary entities within the *U. acanthinura* group as valid on specific level: *U. alfredschmidti*, *U. geyri*, *U. acanthinura*, *U. nigriventris* and *U. dispar*. This result is in general accordance with the results of AMER & KUMAZAWA (2005) and HARRIS et al. (2007).

The second group within the genus *Uromastyx* comprising several nominal taxa and only showing a weak morphological and genetic differentiation is the *Uromastyx aegyptia* group. Within this group four nominal taxa are known: *aegyptia*, *leptieni*, *microlepis* and *occidentalis*. We hypothesize that the origin of the *U. aegyptia* group is Africa and that the Arabian radiation of this group has only recently dispersed into the Arabian Peninsula. The clarification of the evolutionary scenario of the *U. aegyptia* group would require the incorporation of *U. occidentalis* in the genetic analysis and the resolution of the relationships between all identified species groups. A sister group relationship between the *U. acanthinura* and the *U. aegyptia* group as postulated on the basis of morphological data (MOODY 1987; WILMS 2001; this study) would bring the groups together, which represent the most recent evolutionary lineages.

Despite the overall similarity of the taxa of the *U. aegyptia* group, it is possible to differentiate between them on the basis of morphological characters (WILMS & BÖHME 2001, 2007). Genetically, they exhibit the following intertaxon distances: *aegyptia-microlepis*: 0.3–0.4 %, *microlepis-leptieni*: 0.3–0.6 % and *aegyptia-leptieni*: 0.7–0.9 %. These p-distances based on 12S and 16S rRNA are very low compared to those between *Uromastyx* species in general, but are similar to those shown by the taxa assigned to *U. dispar* as subspecies in the present study. We therefore recognize *Uromastyx aegyptia* as a polytypic species with three subspecies (*aegyptia*, *leptieni*, and *microlepis*). Because of the significant geographic distance between the Arabian *U. aegyptia* and the African *U. occidentalis* we suppose, that both are good species.

The results of the analysis of morphological as well as molecular data for the *U. ocellata* group have been published elswhere (WILMS & SCHMITZ 2007). This group consists of six taxa which represent five evolutionary entities: *benti*, *yemenensis*, *shobraki*, *ocellata*, *ornata*. In the context of the current data, we recognize the subspecies of *U. yemenensis* as valid at specific rank because of the intraspecific genetic distances which are similar between all taxa of the subclade comprising *benti*, *yemenensis* and *shobraki*.

4. TAXONOMY

DEFINITION AND RESURRECTION OF THE GENUS *SAARA* GRAY, 1845

1845 *Saara* Gray, Cat. Spec. Liz. Coll. brit. Mus.: 262. – Type species: *Uromastyx hardwickii* GRAY, 1827

Original definition: Head very short, broad, much arched. Body depressed, with a fold on each side of the back. Scales minute, equal. Tail short, broad, depressed; upper part with cross bands of compressed, conical scales, separated by other rings of granular and smooth square scales; beneath covered with square, smooth, imbricate scales. Femoral pores distinct (GRAY 1845).

Diagnosis: Acrodont dentition, with the premaxillary bone forming in adult specimens a sharp, tooth- like structure replacing the incisive teeth. Tail scalation arranged in distinct whorls, which are separated by 1–6 rows of intercalary scales dorsally.

Species: *Saara asmussi, S. hardwickii, S. loricata.*

Distribution: The species of the genus *Saara* are distributed in eastern Iraq, Iran, Afganistan, Pakistan and northwestern India.

Taxonomy: As shown in the present study, *Saara hardwickii* represents most probably a polytypic species, whose taxa are genetically distinct. Further study on the taxonomy of *Saara hardwickii* is required to evaluate the distribution and morphological characters of the taxa involved.

SYNOPSIS OF THE SPECIES OF THE GENUS *SAARA* GRAY, 1845

***Saara asmussi* (Strauch, 1863) new comb.**
[Common name: Persian Spiny-tailed Lizard]

Centrotrachelus asmussi STRAUCH, 1863; Bull. Acad. Sci. St. Pétersbourg, 6: 479.

Uromastix asmussi – BOULENGER 1885; Cat. Liz. brit. Mus., 1: 409.

Uromastyx asmussi – MERTENS 1956; Jh. Ver. vaterl. Naturk. Württemb., 111: 93.

Holotype: ZISP 3029 (Zoological Museum, Academy of Sciences, Russian Academy of Sciences, St. Petersburg), male, Seri-Tschah (Eastern Persia), coll. Keyzerling, 1858–1859.

Differential diagnosis: The species *asmussi* belongs to the genus *Saara.* This taxon is distinguished from *Saara hardwickii* by having 1–2 rows of unkeeled intercalary scales separating each tail whorl dorsally (2–6 keeled intercalary scales in *S. hardwickii*). *S. asmussi* is distinguished from *S. loricata* in having fewer preanofemoral-pores (8–13 in *S. asmussi* vs. 14–20 in *S. loricata*).

Subspecies: None

Description: Maximum total length 475 mm, maximum SVL 265 mm. 170–201 scales around mid-body, 94–103 scales between gular- and inguinal fold, 40–53 gular scales, 21–27 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–7 scales between supralabial and enlarged subocular scale. 25–30 scales around 5th whorl. 23–26 tail whorls. 11–13 scales beneath 4th left toe. 8–13 preanofemoral pores on either side.

Colouration: Head, shoulders and forelegs coloured light grey to blue. Hindlegs yellowish grey to blue. Tail dull grey-olive with yellowish spines or completely blue. Back light ocker yellow up to the tailroot; some tubercules on the back are coloured orange. The belly is yellowish white with dark spots on the breast. At low temperatures the back is blackgrey. For pictures of live animals see ANDERSON (1999).

Distribution: *Saara asmussi* lives in the dry areas of Iran, Afghanistan and Pakistan. In Iran the species lives in the following provinces: Esfehan, Kerman, Khorasan and Baluchistan-Sistan (ANDERSON 1974, 1999). In Pakistan the species is known from Baluchistan (MINTON 1966, KAHN 1980). The presence in Afghanistan obviously is limited to the southern part of the country in the bordering area with Iran and Pakistan (for map see ANDERSON 1999 and WILMS 2001).

***Saara hardwickii* (Gray, 1827)**
[Common name: Indian Spiny-tailed Lizard]

Uromastix hardwickii Gray, 1827; in HARDWICKE & GRAY, Zool. J. 3: 219.

Uromastix griseus Cuvier, 1829; Règne animal, Ed. 2, 2: 34.

Uromastix reticulatus Cuvier, 1829; (nomen nudum; syn. fide BOULENGER 1885), Règne animal, Ed. 2, 2: 34.

Uromastyx grisseus – GRAY 1831; GRAY (ex errore) in GRIFFITH, Animal Kingdom of Cuvier 9 Synops. Spec.: 62.

Centrocercus griseus – FITZINGER 1843; (non *Centrocercus* SWAINSON 1831 = Aves), Syst. Rept. 1: 18, 86.

Uromastyx similis Fitzinger, 1843; (nomen nudum; syn. fide BOULENGER 1885), Syst. Rept., 1: 86

Saara hardwickii – GRAY 1845; Cat. Spec. Liz. Coll. brit. Mus.: 262.

Uromastyx hardwickii – KAHN 1980; Biologica 26 (1/2): 133.

Uromastyx hardwickü – SHARMA 1992; Cobra, Madras Snake Park Trust 10: 8 (error typographicus).

Holotype: BMNH 1946.8.14.44, male, Plains of Kanouge, Hindustan, India, pres. General Hardwicke, without date.

Differential diagnosis: The species *hardwickii* is the type species of the genus *Saara.* This taxon is distinguished from *S. asmussi and S. loricata* by having 2–6 keeled intercalary scales separating each tail whorl dorsally (1–2 rows of unkeeled intercalary scales in *S. asmussi and S. loricata*).

Subspecies: None

Description: Maximum total length 438 mm, maximum SVL 233 mm. 190–275 scales around mid-body, 112–157 scales between gular- and inguinal fold, 32–46 gular scales, 24–42 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 6-9 scales between supralabial and enlarged subocular scale. 40–52 scales around 5th whorl. 28–39 whorls. 15–21 scales beneath 4th left toe. 12–19 preanofemoral pores on either side.

Colouration: The colouration of the back is yellow brown, with dark dots or with a vermiculation. The belly is whitish. The throat is scattered with dark dots. The front sides of the upper thighs on both sides show a black spot at the base of the frontlegs. The pattern of the juveniles consists of black dots, which are arranged in a regular way on the back. For pictures of live specimens see WILMS (2005).

Distribution: *Saara hardwickii* is widely distributed in the dry areas of northwest India and Pakistan. In Afghanistan this species lives at least in the border area with Pakistan (near Jalalabad; WILMS 2001).

***Saara loricata* (Blanford, 1874) new comb.**
[Common name: Iraqi Spiny-tailed Lizard]

Centrotrachelus loricatus Blanford, 1874; Proc. zool. Soc. London, 1874: 660.

Centrotrachelus asmussi – MURRAY 1884; Ann. Mag. Nat. Hist. 14 (Ser.5): 101.

Uromastix loricatus – BOULENGER 1885; Cat. Liz. brit. Mus., 1: 409.

Uromastix costatus Müller, 1885; Verh. natforsch. Ges. Wien 7: 292 & 713 (syn. fide BOULENGER, Zool. Rec. 1885).

Uromastyx asmussi loricatus – MERTENS 1956; Jh. Ver. vaterl. Naturk. Württemb., 111: 93.

Uromastyx loricatus – CLARK, CLARK & ANDERSON 1966; Occ. Pap. Calif. Acad. Sci. 55: 6.

Centrotrachelis loricatus – HAAS & WERNER 1969; Bull. Mus. Comp. Zool., 138 (6): 341.

Uromastyx loricata – WILMS 1995; Dornschwanzagamen: 95.

Holotype: BMNH 1946.8.11.59, female, Bushir, Iraq, pres. P.L. Sclater, without date.

Differential diagnosis: This taxon is distinguished from *Saara hardwickii* by having 1–2 rows of unkeeled intercalary scales separating each tail whorl dorsally (2–6 keeled intercalary scales in *S. hardwickii*). *S. loricata* is distinguished from *S. asmussi* in having more preanofemoralpores (8–13 in *S. asmussi* vs. 15–20 in *S. loricata*).

Subspecies: None

Description: Maximum total length 520 mm, maximum SVL 290 mm. 183–234 scales around mid-body, 101–110 scales between gular- and inguinal fold, 32–45 gular scales, 24–36 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–8 scales between supralabial and enlarged subocular scale. 23–33 scales around 5th whorl. 22–26 tail whorls. 11–13 scales beneath 4th left toe. 15–20 preanofemoral pores on each side.

Colouration: Head, limbs, back and tail brown, yellow-grey or crème coloured with small intermixed brown dots. Back sometimes vividly red coloured. The belly is yellow brown or yellowish white (KALAF 1959; HAAS & WERNER 1969). For pictures of live animals see ANDERSON (1999).

Distribution: *Saara loricata* lives in the arid areas of Iraq and southwest Iran. In Iran the following provinces are inhabitated: Kurdestan-Kermanshah, Kuzestan-Lorestan and Fars (ANDERSON 1974).

DEFINITION OF THE GENUS *UROMASTYX* MERREM, 1820

1820 *Uromastyx* MERREM, Tent. Syst: 56. – Type species (fide FITZINGER 1843): *Stellio spinipes* Daudin = *Uromastyx aegyptia* (ForsskÅl)

Original definition: Cauda squamis magnis crassis aculeatis verticillata (Tail annulated by large, thick and spiny scales) (MERREM 1820).

Diagnosis: Acrodont dentition, with the premaxillary bone forming in adult specimens a sharp, tooth- like structure replacing the incisive teeth. Tail scalation arranged in distinct whorls, which are not separated by intercalary scales dorsally.

Species: *Uromastyx acanthinura, U. aegyptia, U. alfredschmidti, U. benti, U. dispar, U. geyri, U. nigriventris, U. ornata, U. ocellata, U. occidentalis, U. princeps, U. macfadyeni, U. shobraki, U. thomasi, U. yemenensis.*

Distribution: The species of the genus *Uromastyx* are distributed in all North African countries bordering the Sahara desert (Algeria, Chad, Egypt, Libya, Mali, Mauritania, Morocco, Niger, Sudan, and Tunesia) as well as in Ethiopia, Eritrea, Djibouti and Somalia in Africa and in all countries on the Arabian Peninsula. In the north *Uromastyx* occures in Israel, Jordan, Syria, Iraq and to the east on a narrow stripe along the Arabian Gulf in Iran (up to the city of Bandar Abbas).

Taxonomy: Within the genus *Uromastyx* several taxonomic problems remain unresolved. Further studies should focus on the phylogenetic relationships between and within the different species groups (eg. *U. o. ornata* and *U. o. philbyi*) as well as on the evaluation of the taxonomic placement of *U. princeps*, *U. macfadyeni*, *U. alfredschmidti* and *U. occidentalis* within the genus.

SYNOPSIS OF THE SPECIES OF THE GENUS *UROMASTYX* MERREM, 1820

Uromastyx acanthinura Bell, 1825

[Common name: North African Spiny-tailed Lizard]

Uromastyx acanthinurus Bell, 1825; Zool. J., 1:457.

Uromastix mutabilis – FISCHER 1885; Zool. Garten 26: 272.

Uromastix acanthinurus – BOULENGER 1885; Cat. Liz. Brit. Mus. Vol. 1: 406.

Uromastix acanthinurus nigerrimus – HARTERT, 1913; Novitat. Zool. Tring 20: 79.

Uromastyx acanthinurus acanthinurus – MERTENS 1962; Senckenberg. biol. 43: 426.

Uromastyx acanthinura acanthinura – WILMS 1995; Dornschwanzagamen: 57.

Holotype: OUM 7845 (Oxford University Museum of Natural History), N. Africa (brought by Capt. Lyon RN), Bell & Hope Collection.

Differential diagnosis: *U. acanthinura* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (50.27–74.42 % of SVL in *U. acanthinura* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and from *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row in *U. acanthinura*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia*, 297–301 in *U. occidentalis* vs. 146–195 in *U. acanthinura*), from *U. geyri* and *U. alfredschmidti* by the shorter tail (50.27–74.42 % of SVL in *U. acanthinura* vs. 65.45–98.06 % in *U. geyri* and 79.31–87.26 % in *U. alfredschmidti*). Diagnostic characters between *U. acanthinura* and the subspecies of *U. dispar* are: Lower number of scales around midbody [145–195 (mean. 165.6) in *U. acanthinura* vs. 187–227 (mean: 205.0) in *U. d. dispar*]; lower number of ventrals [74–96 (mean. 83.1) in *U. acanthinura* vs. 88–118 (mean: 104.5) in *U. d. flavifasciata*] and lower number of subdigital scales [9–15 (mean: 12.7) in *U. acanthinura* vs. 15–18 (mean: 16.4) in *U. d. maliensis*]. *U. acanthinura* is differentiated from *U. nigriventris* by being much less colourful and lacking red, green and citreous colouration.

Subspecies: None

Description: Maximum total length 430 mm, maximum SVL 253 mm. 146–195 scales around midbody, 74–96 scales between gular- and inguinal fold, 25–45 gular scales, 22–38 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–8 scales between supralabial and enlarged subocular scale. 26–32 scales around 5th whorl. 16–20 tail whorls. 9–15 scales beneath 4th left toe. 10–16 preanofemoral pores on each side.

Colouration: Pattern and colouration of *U. acanthinura* is not very variable. There is a sexual dimorphism with males being black with white or yellowish dots and females being beige to silvergrey with small dark spots. For pictures of live specimens see SCHLEICH et al. (1996) and WILMS (2005).

Distribution: *U. acanthinura* lives at the northern edge of the Sahara, but penetrades deep into the central Sahara along wadis or along plateaus and mountain chains. Geographically it occurs in the dry areas of eastern Algeria, Tunesia and northwest Libya. For detailed discussion of the distribution of this taxon and for a distribution map see WILMS (2005). Further studies are needed to assess the geographic distribution of *U. acanthinura* and *U. nigriventris* in the area between the Great Ergs (Grande Erg Occidental and Grande Erg Oriental).

Uromastyx aegyptia Forsskål, 1775

[Common names: Egyptian Spiny–tailed Lizard]

Differential diagnosis: *U. aegyptia* is distinguished from *U. thomasi* and *U. princeps* by the longer tail (60.18–102.83 % of SVL in *U. aegyptia* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and from *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–8 whorls forming a continuous scale row in *U. aegyptia*; from the species of the *U. acanthinura* group by more scales around midbody (238–322 in *U. aegyptia* vs. 142–231 in the species of the *U. acanthinura* group). *U. aegyptia* is distinguished from *U. occidentalis* by having preanofemoral pores.

Subspecies: We recognize three of the closely related taxa within the *U. aegyptia* clade as subspecies of one single species: *U. aegyptia aegyptia, U. a. microlepis and U. a. leptieni*. The phylogenetic relationship of the nominal species *U. occidentalis* requires further studies based on new material.

Uromastyx aegyptia aegyptia (Forsskål, 1775)

Lacerta aegyptia Forsskål, 1775; Descr. Anim. Itin. orient.: 13.

Lacerta harbai Forsskal, 1775; Descr. Anim. Itin. orient.: 9 (? syn. fide MERREM 1820).

Stellio spinipes Daudin, 1802; Hist. nat. gén. part. Rept. 4: 31.

Uromastyx spinipes – MERREM 1820; Tent. Syst. Amph.: 56.

Lacerta herbai – MERREM 1820; Tent. Syst. Amph.: 56 (nomen substitutum pro *Lacerta harbai* Forsskål, 1775).

Mastigura spinipes – FLEMING 1822; Philos. Zool., 2: 277.

Uromastix spinipes – BOULENGER 1885; Cat. Liz. brit. Mus. 1: 407.

Uromastix aegyptius – ANDERSON 1896; Contrib. Herpetol. Arabia: 79, 85.

Uromastyx aegyptia – FLOWER 1933; Proc. zool. Soc. London 1933: 779.

Uromastyx aegyptius – WERNER 1982; Herp. Comun.,Wildl. Res. Rep. 13: 155.

Uromastyx aegyptius aegyptius – ARNOLD 1987; Proc. Symp. Fauna Zoogeogr. Middle East. 28: 249.

Uromastyx aegyptia – SCHÄTTI & GASPARETTI 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx aegyptia aegyptia – WILMS 1995; Dornschwanzagamen: 71.

Neotype: ZFMK 44216, adult male, Suez at the road to Cairo, Egypt, coll. I. REHAK, VIII. 1982 (designated by WILMS & BÖHME 2000 a).

Differential diagnosis: The nominotypic subspecies is distinguished from *U. a. microlepis* by having enlarged tubercular scales scattered over the scalation of the flanks and by lower scale counts. It is distinguished from *U. a. leptieni* by a different juvenile colour pattern and a higher number of ventrals (see WILMS & BÖHME 2000 a).

Description: Maximum total length exceeding 700 mm. 247–322 scales around midbody, 126–158 scales between gular- and inguinal fold, 33–59 gular scales, 24–31 scales from the mid of the lower end of the ear opening to the mental scale. On both sides 4–7 scales between supralabial and enlarged subocular scale. 29–46 scales around 5th whorl. 20–23 tail whorls. 16–20 scales beneath 4th left toe. 14–20 preanofemoral pores on either side.

Colouration: *U. aegyptia* has the ability of a physiological colour change. At high temperatures the animals show a light brown to light grey coloration with a black throat and small black dots on the neck. Some individuals have an entirely black to dark blue colouration of the head. At low temperatures the animals show a dark grey, nearly black, colouration. Juveniles have characteristic transverse rows of yellow to orange ocelli on their back. The main colouration of the body is greyish brown. For pictures of live specimens see WILMS (2005).

Distribution: The nominotypic subspecies inhabits nothern Egypt east of the river Nile, the Sinai Peninsula, Palestina and extreme northwestern Saudi Arabia (Wadi Sawawin / Jabal as Sinfa). The border between the ranges of the taxa *aegyptia* and *microlepis* is obviously east of Wadi Araba in Palestina and Jordan and east of Wadi Sawawin in the Jabal as Sinfa region of Saudi Arabia.

***Uromastyx aegyptia microlepis* Blanford, 1874**
Uromastix microlepis Blanford, 1874; Proc. zool. Soc. London, 1874.

Uromastyx microlepis – SCHMIDT 1939; Field Mus. nat. Hist. Zool. 24: 59.

Uromastyx aegyptius – SCHMIDT 1941; Field Mus. nat. Hist. Zool. 24 (16): 162.

Uromastyx aegyptius microlepis – MERTENS 1956; Jh. Ver. vaterl. Naturk. Württemb., 111: 93.

Uromastix aegyptius – KEVORK & AL-UTHMAN 1972; Bull. Iraq Nat. Hist. Mus. 5 (2): 26.

Uromastyx aegyptius – MOODY 1987; Proc. 4th General Meeting of the Societas Europaea Herpetologica: 287.

Uromastyx aegyptia – SCHÄTTI & GASPARETTI 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx aegyptia microlepis – WILMS 1995; Dornschwanzagamen: 72.

Lectotype: BMNH 1946.8.14.55, adult male, Basrah, Iraq, leg. Capt. Phillips, without date (designated by WILMS & BÖHME 2000 a).

Differential diagnosis: *Uromastyx a. microlepis* is distinguished from *U. a. aegyptia* by lacking enlarged tubercular scales scattered over the scalation of the flanks and by smaller scales. It is distinguished from *U. a. leptieni* by a different juvenile colour pattern and a higher number of ventrals (see WILMS & BÖHME 2000 a).

Description: Maximum total length exceeding 700 mm. 255–391 scales around mid-body, 149–193 scales between gular- and inguinal fold, 38–65 gular scales, 27–49 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–8 scales between supralabial and enlarged subocular scale. 30–43 scales around 5th whorl. 20–24 tail whorls.14–23 scales beneath 4th left toe. 13–21 preanofemoral pores on either side.

Colouration: *U. aegyptia microlepis* has the ability of physiological colour change. At high temperatures the animals show a light brown to yellow or greenish coloration with a black throat and small black dots on the neck and dorsum. Some individuals have an entirely black to dark blue colouration of the head. At low temperatures the animals show a dark grey, nearly black, colouration. For pictures of live specimens see Wilms (2005) and Sindalco & Jeremčenko (2008).

Juveniles have characteristic transverse rows of yellow to orange ocellae on their back. The main colouration of the body is greyish brown.

Distribution: *Uromastyx aegyptia microlepis* lives in the deserts and semideserts of Arabia (Saudi Arabia, Yemen, Oman, United Arab Emirates, Qatar, Kuwait), in Jordan, Syria, Iraq and coastal Iran.

***Uromastyx aegyptia leptieni* Wilms & Böhme, 2000 new status**

Uromastyx leptieni Wilms & Böhme, 2000; Herpetozoa 13(3/4): 142.

Uromastyx leptiens – Harris, Vaconcelos & Brito 2007; Amphibia-Reptilia 28 (2007): 1 (error typographicus).

Holotype: ZFMK 52398, adult female, Wadi Siji, United Arab Emirates (UAE), coll. R. Leptien, VI. 1983.

Differential diagnosis: *Uromastyx a. leptieni* is distinguished from *aegyptia* and *microlepis* by a different juvenile colour pattern and a lower number of ventrals (see Wilms & Böhme 2000 a).

Description: Maximum total length 675 mm. 238–294 scales around mid-body, 112–130 scales between gular- and inguinal fold, 40–47 gular scales, 30–37 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–7 scales between supralabial and enlarged subocular scale. 32–37 scales around 5th whorl. 22–24 tail whorls. 17–21 scales beneath 4th left toe. 12–19 preanofemoral pores on either side.

Colouration: Main colour olive-beige with small dark dots. Neck, head and throat black. In some specimens the throat is marbled with black and orange. Ventral part of the front-legs, chest and belly marbled with grey. Ventral parts of the hind legs and first half of the tail grey.

Colouration of juveniles red brown to dark brown with a dark brown to black net-like pattern. For pictures of live specimens see Wilms (2005) and Wilms & Böhme (2007).

Distribution: *Uromastyx aegyptia leptieni* is known from east of the Hajar al-Gharbi mountains in northern Oman (from the vicinity of Muscat up to the Musandam peninsular), and from north-eastern United Arab Emirates. The westernmost locality is near Abu Dhabi Airport (24° 27' N 54°38'E). For detailed distribution maps for the taxa assigned here to the species *Uromastyx aegyptia* on subspecific level see Wilms & Böhme (2007).

***Uromastyx alfredschmidti* Wilms & Böhme, 2001**
[Common name: Schmidt's Spiny-tailed Lizard]

Uromastyx acanthinurus – Joger 1981; Bonn. Zool. Beitr. 32 (3–4): 323.

Uromastyx alfredschmidti Wilms & Böhme, 2001; Zool. Abh. 51 (1): 95.

Holotype: ZFMK 24643, adult male, Tassili N'Ajjer, Tamrit Plateau (1600 m), approx. 30 km northeast Djanet, Algeria, leg. Dr. G. Wangorsch, 22.07.1974.

Differential diagnosis: *U. alfredschmidti* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (79.31–87.26 % of SVL in *U. alfredschmidti* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–3 whorls forming a continuous scale row in *U. alfredschmidti*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia,* 297–301 in *U. occidentalis* vs. 138–202 in *U. alfredschmidti*), from *U. acanthinura, U. nigriventris* and *U. dispar* by its longer tail (79.31–87.26 % of SVL in *U. alfredschmidti* vs. 50.27–74.42 in *U. acanthinura*, 47.83–70 % in *U. dispar* and 43.48–75.14 % in *U. nigriventris*). From *U. geyri* it is distinguished by differences in the scalation of the flanks (enlarged triangular and imbricate scales in *U. alfredschmidti* vs. enlarged tubercular scales in *U. geyri*), as well as the complete black colouration of adult males in *U. alfredschmidti*.

Subspecies: None

Description: Maximum total length 429 mm, maximum SVL 230 mm. 138–202 scales around midbody, 68–94 scales between gular- and inguinal fold, 26–42 gular scales, 17–36 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–6 scales between supralabial and enlarged subocular scale. 28–32 scales around 5th whorl. 21–24 tail whorls. 12–15 scales beneath 4th left toe. 13–21 preanofemoral pores on each side.

Colouration: Adult males are entirely black. One female from the type-series has a lightbrown colour, with throat and rear part of the abdomen being ivory-coloured with a light brown reticulation. The top of the tail is coloured dark brown. Adult females can also be totally black. For pictures of live specimens see WILMS (2005) and SINDALCO & JEREMČENKO (2008).

Distribution: *U. alfredschmidt* is restricted to the Tamrit plateau, the Hoggar Mountains in southern Algeria and the Akkakus region in southwestern Libya (for distribution map see WILMS & BÖHME 2001)

***Uromastyx benti* (Anderson, 1894)**
[Common name: Yemeni Spiny-tailed Lizard]

Aporoscelis benti Anderson, 1894; Ann. Mag. nat. Hist., London, (6) 14: 376.

Uromastix (*Aporoscelis*) *benti* – ANDERSON 1896; Contrib. Herpetol. Arabia: 33.

Uromastix simonyi Steindachner, 1899; Anz. Akad. Wiss. Wien. math. naturwiss. Kl., 36: 143

Uromastyx benti – PARKER 1938; Ann. Mag. Nat. Hist. (11) 1: 486.

Aporoscelis benti – SCHMIDT 1939; Field Mus. nat. Hist. Zool. 24: 59.

Uromastix philbyi – HAAS & BATTERSBY 1959; Copeia 1959: 202 (syn. fide ARNOLD 1986).

Uromastyx thomasi – AL-BADRY & AL-SAFADI 1982; Proc. Egypt. Acad. Sci 34: 66 (syn. fide SCHÄTTI 1989).

Uromastyx (*Aporoscelis*) *benti* – JOGER 1987; Proc. Symp. Fauna Zoogeogr. Middle East. 28: 260.

Uromastyx ocellata benti – SCHÄTTI & GASPARETTI, 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – SCHÄTTI & DESVOIGNES 1999; The Herpetofauna of southern Yemen and the Sokotra Archipelago: 39.

Lectotype: BMNH 1946.8.11.72, adult male, Wadi Hadramaut, Yemen, leg. Dr. J. Anderson, without date (designated by WILMS & BÖHME 2000 b).

Differential diagnosis: *Uromastyx benti* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group and *U. macfadyeni*) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. ocellata*, *U. ornata* and *U. macfadyeni* the species differs in lacking femoral- and preanalpores.

Uromastyx benti differs from *U. shobraki* and *U. yemenensis* in having larger scales around midbody (188.92 +/- 13.22 in *U. shobraki*, 197.44 +/- 20.9463 in *U. yemenensis* vs. 160.05 +/- 8.98 in *U. benti*) and larger ventrals (86.64 +/- 4.88 in *U. shobraki*, 88.25 +/- 6.98 in *U. yemenensis* vs. 74 +/- 4.02 in *U. benti*), but also in significant genetic differences.

Subspecies: None

Description: Maximum total length 360 mm, maximum SVL 196 mm. 143–187 scales around midbody, 66–86 scales between gular- and inguinal fold, 23–33 gular scales, 19–27 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–7 scales between supralabial and enlarged subocular scale. 28–38 scales around 5th whorl. 22–26 tail whorls. 11–15 scales beneath 4th left toe. No preanofemoral pores.

Colouration: Ground colour of the males back, tail and hind legs yellowish brown. Tail without distinct pattern, hind legs with a turquoise and orange colouration. Back with a pattern consisting of dark brown lines and dots, as well as 7–9 rows of ocellae (ivory coloured with dark brown edges); Dorsal side of the front legs anthracite coloured with orange and green colour elements. Hands yellowish brown. Head orange, dark brown and black marbled. Underside of the head anthracite coloured with some orange dots. Ventral parts of forelegs and chest marbled with grey. Belly with narrow grey/anthracite crossbands. The females are much paler in colouration, with a yellowish brown ground colour and a pattern of small dark brown lines and dots. For pictures of live specimens see WILMS & BÖHME (2007) and SINDALCO & JEREMČENKO (2008).

Distribution: *Uromastyx benti* occurs in southern and southeastern Yemen, from the vicinity of Azzan eastwards to the Hadramaut Valley and along the coast of the Arabian Sea. In the Sultanate of Oman this species is only known from the vicinity of Mirbat in south-western Oman (SEUFER et al. 1998, WILMS & HULBERT 2000).

***Uromastyx dispar* Heyden, 1827**
[Common name: Southern Saharan Spiny-tailed Lizard]

Differential diagnosis: *U. dispar* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (43.83–70 % of SVL in *U. dispar* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row in *U. dispar*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia,* 297–301 in *U. occidentalis* vs. 164–231 in *U. dispar*), from *U. geyri* and *U. alfredschmidti* by the shorter tail (43.83–70 % of SVL in *U. dispar* vs. 65.45–98.06 % in *U. geyri* and 79.31–87.26 % in *U. alfredschmidti*). Diagnostic characters between *U. acanthinura, U. nigriventris* and the subspecies of *U. dispar* are: Lower number of scales around midbody [145–195 (mean. 165.6) in *U. acanthinura*, 139–208 (mean: 170.63) in *U. nigriventris* vs. 187–227 (mean: 205) in *U. d. dispar*]; lower number of ventrals [74–96 (mean. 83.1) in *U. acanthinura*, 66–99 (mean: 83.98) in *U. nigriventris* vs. 88–118 (mean: 104.5) in *U. d. flavifasciata*] and lower number of subdigital scales [9–15 (mean: 12.7) in *U. acanthinura*, 9–17 (mean: 13.15) in *U. nigriventris* vs. 15–18 (mean: 16.4) in *U. d. maliensis*]. For a detailed discussion of the differences between *acanthinura*, *nigriventris*, *dispar*, *flavifasciata* and *maliensis* see Wilms & Böhme (2001).

Subspecies: We recognize three of the closely related taxa within the *U. acanthinura* clade as subspecies of *U. dispar*: *U. d. dispar, U. d. flavifasciata* and *U. d. maliensis*.

***Uromastyx dispar dispar* Heyden, 1827**
Uromastyx dispar Heyden, 1827; Atl. Reise nördl. Afr. Rept.: 5.

Uromastix acanthinurus – Wake & Kluge 1961; Contr. Sci. No. 40: 11.

Uromastyx acanthinurus dispar – Mertens 1962; Senckenb. biol. 43: 430.

Holotype: SMF 10417, female, Desert near Ambukol and Dongola, Sudan, coll. E. Rüppel, 1826.

Differential diagnosis: Discrimination between the subspecies of *U. dispar* is possible only by means of colouration of adult males. Adult *U. d. dispar* males are distinguished from adult *U. d. flavifasciata* males by lacking transversal stripes on the animals back and from adult *U. d. maliensis* males by the less pronounced black colouration of the body.

Description: Maximum total length 376 mm, maximum SVL 231 mm. 187–227 scales around midbody, 79–103 scales between gular- and inguinal fold, 30–43 gular scales, 24–33 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–8 scales between supralabial and enlarged subocular scale. 30–36 scales around 5th whorl. 16–21 tail whorls. 12–18 scales beneath 4th left toe. 11–18 preanofemoral pores on each side.

Colouration: Adult males of *U. d. dispar* show a black colouration of limbs, heads and tails. Dorsal colouration is yellow or yellowish green. Females are sand coloured with small black dots and occasionally 4–5 grey bars at the flanks. For pictures of live specimens see Wilms et al. (2003) and Wilms (2005).

Distribution: *U. dispar dispar* is found in the desert areas west of the Nile in Sudan and in the Tibesti and Ennedi mountains in Chad. The northernmost locality is Wadi Halfa at the border beween Sudan and Egypt. This taxon has not been found in Egypt yet (contra Saleh 1997). In the Ennedi Mountains, *U. d. dispar* is known from Fada, while it is known from Bardai and Zouar in the Tibesti Mountains. Between the Ennedi and Tibesti this taxon is known from Ouniaga/Erdi. The westernmost location is Zouar (western Chad).

***Uromastyx dispar flavifasciata* Mertens, 1962**
Uromastyx acanthinurus flavifasciatus Mertens, 1962; Senckenb. biol. 43: 427.

Uromastyx acanthinura acanthinura – Wilms 1995; Dornschwanzagamen: 57.

Uromastyx acanthinura flavifasciata – Schleich, Kästle & Kabisch 1996; Amph. & Rept.of North Africa: 309.

Uromastyx flavifasciata flavifasciata – Mateo, Geniez, López-Jurado & Bons 1998; Rev. Esp. Herp. 12: 104.

Uromastyx flavifasciata obscura Mateo, Geniez, López-Jurado & Bons, 1998; Rev. Esp. Herp. 12: 104.

Uromastyx dispar flavifasciata – Wilms & Böhme 2001; Zool. Abh. 51 (1): 88.

Uromastyx flavifasciata – Geniez, Mateo, Geniez & Pether 2004; Amph. & Rept. of the Western Sahara: 94.

Holotype: SMF 58032, male, approx. 50 km north of Dakar, Senegal (For the reliability of the type locality see Böhme 1978), coll. N. Heidrich, 01.11.1961.

Differential diagnosis: Adult *U. d. flavifasciata* males can be distinguished from *U. d. dispar* and *U. d. maliensis* males by their black body colouration with 5–7 wide, clearly-defined yellow, white or red dorsal crossbands. Occasionally these crossbands can be reduced or be even completely absent.

Description: Maximum total length 455 mm, maximum SVL 280 mm. 164–231 scales around midbody, 88–118 scales between gular- and inguinal fold, 37–48 gular scales, 27–36 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–6 scales between supralabial and enlarged subocular scale. 31–37 scales around 5th whorl. 19–21 tail whorls. 14–18 scales beneath 4th left toe. 13–17 preanofemoral pores on each side.

Colouration: Adult males of *Uromastyx dispar flavifasciata* show black body colouration with 5–7 wide, clearly-defined yellow, white or red dorsal crossbands, which can occassionally, be absent. Females are sand colored with small black dots and ocelli at their backs. For pictures of live specimens see WILMS et al. (2003) and WILMS (2005).

Distribution: *Uromastyx dispar flavifasciata* lives in the Western Sahara south of 28° northern latitude, in Mauritania and in southwestern Algeria.

Uromastyx dispar maliensis **Joger & Lambert, 1996**
Uromastix acanthinurus – ANDERSSON 1935; K. Vet. O. Vitterh. Samh. Handl. Ser. B. 4 (10): 9.

Uromastyx acanthinurus – PAPENFUSS 1969; Wasman Jour. Biol. 27 (2): 286.

Uromastyx sp. – JOGER 1986; Studies in Herpetology: 187.

Uromastyx maliensis Joger & Lambert, 1996; J. Afr. Zool. 110 (1): 24.

Uromastyx dispar maliensis – WILMS & BÖHME 2001; Zool. Abh. 51 (1): 89.

Holotype: HLMD RA 1545, female, 40 km southeast of Gao, Mali, coll. H. Rudolf, without date.

Differential diagnosis: Adult *Uromastyx dispar maliensis* males differ from adult *dispar* males by the more pronounced black colouration of the body and from adult *flavifasciata* males by lacking transversal crossbands on the dorsum.

Description: Maximum total length 383 mm, maximum SVL 232 mm. 177–224 scales around midbody, 86–112 scales between gular- and inguinal fold, 34–46 gular scales, 30–40 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 5–9 scales between supralabial and enlarged subocular scale. 30–38 scales around 5th whorl. 16–20 whorls. 15–18 scales beneath 4th left toe. 11–17 preanofemoral pores on each side.

Colouration: Dorsal colouration in adult male *maliensis* consists of yellow ocelli on a dark ground colour. The ocelli may merge partially, though they never form crossbands. Adult females are brownish black with a beige-yellow to yellow dorsal coloration, which may have dark brown to brownish black vermiculation or ocelli. For pictures of live specimens see JOGER & GRAY (1997), WILMS & MÜLLER (1998) and WILMS (2005).

Distribution: *U. dispar maliensis* lives in northwestern Mali, in the Tilemsi Valley, on the edge of the Adrar des Iforas and in southwestern Algeria (Taoudrart in Tanezrouft). *U. dispar maliensis* und *U. geyri* occur sympatrically in the region of the Adrar des Iforas (JOGER & LAMBERT 1996). The northernmost locality of *U. d. maliensis* is Gara Djenoum / Hoggar Mountains (WILMS & BÖHME 2001).

Uromastyx geyri **Müller, 1922**
[Common name: Geyr's Spiny-tailed Lizard]

Uromastix temporalis Valenciennes, 1854; C. R. Acad. Sci. 39: 89.

Uromastix acanthinurus nigerimmus – GEYR VON SCHWEPPENBURG 1917; J. Ornith. 65 (3): 286 (error typographicus).

Uromastix geyri MÜLLER, 1922; Naturwiss. Beobachter 63: 193.

Uromastyx acanthinurus geyri – MERTENS 1962; Senckenb. biol. 43: 430.

Uromastyx geyri – JOGER 1981; Bonn. zool. Beitr. 32 (3–4): 324.

Uromastyx acanthinura geyri – WILMS 1995; Dornschwanzagamen: 61.

Uromastyx (*acanthinura*) *geyri* – JOGER & LAMBERT 1996; Jour. Afr. Zool. 100(1): 24.

Neotype: ZFMK 9230 (designated by MÜLLER 1951), male, Gara Djenoum, Ahaggar Mts. Algeria, S Algeria, coll. Frhr. Hans Geyr von Schweppenburg, 10 March 1914.

Differential diagnosis: *U. geyri* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (65.45–98.06 % of SVL in *U. geyri* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row in *U. geyri*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia,* 297–301 in *U. occidentalis* vs. 142–196 in *U. geyri*), from *U. acanthinura, U. nigriventris* and *U. dispar* by its longer tail (65.45–98.06 % of SVL in *U. geyri* vs. 50.27–74.42 in *U. acanthinura*, 47.83–70 % in *U. dispar* and 43.48–75.14 % in *U. nigriventris*). From *U. alfredschmidti* it is distinguished by differences in the scalation of the flanks (enlarged triangular and imbricate scales in *U. alfredschmidti* vs. enlarged tubercular scales in *U. geyri*), as well as the complete black colouration of adult males in *U. alfredschmidti*.

Subspecies: None

Description: Maximum total length 355 mm, maximum SVL 193 mm. 142–196 scales around midbody, 69–93 scales between gular– and inguinal fold, 22–40 gular scales, 19–28 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–4 scales between supralabial and enlarged subocular scale. 23–32 scales around 5th whorl. 20–23 tail whorls. 13–17 scales beneath 4th left toe. 13–20 preanofemoral pores on each side.

Colouration: *Uromastyx geyri* shows only a limited variability. The animals are either beautifully vermilion red or shiny yellow. The pattern consists of brown to black ornaments, which form a non continuous reticulated pattern, and of transversal rows of eyed-like dots. For pictures of live specimens see LÖHR (2004) and WILMS (2005).

Distribution: Endemic to the Hoggar- and Air mountains, to the Adrar des Iforas in northeastern Mali and southern Algeria as well as to the Tassili N'Ajjer in the vicinity of Amguid. For a distribution map of the species see WILMS (2005).

Uromastyx macfadyeni Parker, 1932
[Common name: Macfadyen's Spiny-tailed Lizard]

Uromastix ocellatus – TORNIER 1905; Zool. Jahrb. Syst., 22 (4): 372 (syn. fide PARKER 1932).

Uromastix ocellatus – NEUMANN 1905; Zool. Jahrb. Syst., 22 (4): 392 (syn. fide PARKER 1932).

Uromastix macfadyeni Parker, 1932; Proc. zool. Soc. London, 1932: 353.

Uromastyx macfadyeni – LANZA 1983; Monit. zool. ital. 8: 208.

Uromastyx ocellata macfadyeni – LANZA 1988; Biogeographia 14: 420.

Uromastyx ocellata ocellata – SCHÄTTI & GASPERETTI 1994; Fauna of Saudi Arabia 14: 369.

Holotype: BMNH 1946.8.14.54, male, near Berbara British Somaliland, Somalia, pres. & coll. V. S. Bryan, without date.

Differential diagnosis: *Uromastyx macfadyeni* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. benti*, *U. shobraki* and *U. yemenensis* the species differs in possessing preanofemoralpores and from *U. ocellata* in having enlarged scales on the anterior margin of the ear opening. From *U. ornata* it is distinguished by a different ratio between tail width at the 5th tail whorl and between 4th and 5th whorl (tail width between the 4th and 5th whorl equivalent to 63–79 % of maximum tail width at the 5th whorl in *U. ornata* vs. tail width between the 4th and 5th whorl equivalent to 56–62 % of maximum tail width at 5th whorl in *U. macfadyeni*).

Subspecies: None

Description: Maximum total length 221 mm, maximum SVL 120 mm. 157–182 scales around midbody, 78–93 scales between gular- and inguinal fold, 29–32 gular scales, 22–27 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–4 scales between supralabial and enlarged subocular scale. 23–26 scales around 5th whorl. 22–23 tail whorls. 14–16 scales beneath 4th left toe. 13–15 preanofemoral pores on each side.

Colouration: Males have an either yellowish, greenish or bluish ground colour, dorsally with a brown or black netlike pattern. The inner areas of these patterns are brightly yellow, brown or bluish. Belly blue or green, partially white. Females are much paler in colouration.

Distribution: *Uromastyx macfadyeni* is known only from the area between Berbera and Heis (20 miles west of Mait) on the Gulf of Aden (Somalia).

Uromastyx nigriventris **Rothschild & Hartert, 1912 new status**
[Common name: Moroccan Spiny-tailed Lizard]

Uromastix acanthinurus nigriventris Rothschild & Hartert, 1912; Novitat. Zool. 18: 468.

Uromastyx acanthinurus werneri Müller, 1922; Naturwissenschaftlicher Beobachter 63: 201.

Uromastyx acanthinurus var. *pluriscutata* Fejérváry, 1927; Ann. Mag. Nat. Hist. 20 (9): 514.

Uromastyx acanthinurus acanthinurus – Bons & Geniez 1996; Amphibiens et Reptiles du Maroc: 126

Holotype: BMNH 1969.2074, male, Tilrhempt between Laghouat and Ghardaia, Algeria, coll. W. Rothschild and E. Hartert, without date (for remarks see Wilms & Böhme 2001).

Differential diagnosis: *U. nigriventris* is distinguished from *U. thomasi* and *U. princeps* by the longer and narrower tail (43.48–75.14 % of SVL in *U. nigriventris* vs. 25.00–36.16 % in *U. thomasi* and 34.62–52.55 % in *U. princeps*); from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row in *U. nigriventris*; from *U. aegyptia* and *U. occidentalis* by the lower scale counts around midbody (238–322 in *U. aegyptia,* 297–301 in *U. occidentalis* vs. 139–208 in *U. nigriventris*), from *U. geyri* and *U. alfredschmidti* by the shorter tail (43.48–75.14 % of SVL in *U. nigriventris* vs. 65.45–98.06 % in *U. geyri* and 79.31–87.26 % in *U. alfredschmidti*). Diagnostic characters between *U. nigriventris* and the subspecies of *U. dispar* are: lower number of scales around midbody [139–208 (mean: 170.63) in *U. nigriventris* vs. 187–227 (mean: 205) in *U. d. dispar*]; lower number of ventrals [66–99 (mean: 83.98) in *U. nigriventris* vs. 88–118 (mean: 104.5) in *U. d. flavifasciata*] and lower number of subdigital scales [9–17 (mean: 13.15) in *U. nigriventris* vs. 15–18 (mean: 16.4) in *U. d. maliensis*]. *U. nigriventris* is differentiated from *U. acanthinura* by being much more colourful, with vividly red, green and citreous coloured specimens.

Subspecies: None

Description: Maximum total length 415 mm, maximum SVL 250 mm. 139–208 scales around midbody, 66–99 scales between gular- and inguinal fold, 26–46 gular scales, 22–35 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–6 scales between supralabial and enlarged subocular scale. 25–36 scales around 5th whorl. 16–21 tail whorls. 9–17 scales beneath 4th left toe. 11–18 preanofemoral pores on each side.

Colouration: In *Uromastyx nigriventris* colouration is very variable, with red, yellow, green and orange coloured specimens. Old adult males show frequently a black colouration of head and belly. For pictures of live specimens see Wilms (2005).

Distribution: *Uromastyx nigriventris* is widespread in Morocco east and south of the Atlas Mountain Chain. In western Algeria it ranges in the Sahara Atlas and in the regions northwest, northeast and southwest of the Great Western Erg. In Morocco the southern distribution limits for this taxon are Oued Draa (Draa-valley) and Djebel Ouarkziz (see also discussion of the distribution of this taxon in Wilms & Böhme 2001).

Uromastyx ornata **Heyden, 1827**
[Common name: Ornate Spiny-tailed lizard]

Differential diagnosis: *Uromastyx ornata* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group and *U. macfadyeni*) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. benti*, *U. shobraki* and *U. yemenensis* the species differs in possessing preanofemoralpores and from *U. ocellata* in having enlarged scales on the anterior margin of the ear opening. From *U. macfadyeni* it is distinguished by a different ratio between tail width at the 5th tail whorl and between 4th and 5th whorl (tail width between the 4th and 5th whorl equivalent to 63–79 % of maximum tail width at the 5th whorl in *U. ornata* vs. tail width between the 4th and 5th whorl equivalent to 56–62 % of maximum tail width at 5th whorl in *U. macfadyeni*).

Subspecies: Based on the high morphological and genetical similarity between *ornata* and *philbyi* we consider both taxa to be conspecific and assign them as subspecies to *Uromastyx ornata*: *U. ornata ornata* and *U. ornata philbyi*.

Uromastyx ornata ornata **Heyden, 1827**
Uromastyx ornatus Heyden, 1827; Atlas Reise nördl. Afr., Rept.: 1.

Uromastix ornatus – Anderson 1896; Contrib. Herpetol. Arabia: 79.

Uromastix oronatus – FARAG & BANAJA 1980; Bull. Fac. Sci. K.A.U. 4: 12 (error typographicus).

Uromastyx ocellatus ornatus – ARNOLD 1986; Fauna of Saudi Arabia 8: 393.

Uromastyx ocellata ornata – LANZA 1988; Biogeographia 14: 420.

Uromastyx ocellata ornata – SCHÄTTI & GASPARETTI 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – SCHÄTTI & DESVOIGNES 1999; The Herpetofauna of south. Yemen and the Sokotra Archipelago: 39.

Holotype: SMF 10403, Mohila = Al Muwaylih, Saudi Arabia, leg. E. RÜPPELL, 1828.

Differential diagnosis: *Uromastyx o. ornata* is distinguished from *U. o. philbyi* by its narrower tail (ratio tail length divided by maximum tail width at the 5th whorl is 3.61–5.3 in *ornata* vs. 3.03–3.96 in *philbyi*).

Description: Maximum total length 368 mm, maximum SVL 196 mm (BMNH 97.10.28.199). 149–185 scales around mid–body, 75–99 scales between gular- and inguinal fold, 22–31 gular scales, 21–27 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–5 scales between supralabial and enlarged subocular scale. 19–25 scales around 5th whorl. 20–23 tail whorls. 11–15 scales beneath 4th left toe. 7–14 preanofemoral pores on each side.

Colouration: *U. ornata* is a very variable species. Colour of the males is green, blue or red, with a irregularly reddish brown net-like pattern and yellow spots on the back. Sometimes yellow cross-bands are present. Ventrum with dark pattern. Females are not as colourful as males. They are light brown with dark brown spots and sometimes light yellow or light red spots. Belly without pattern, yellowish or white. For pictures of live specimens see WILMS et al. (2002), WILMS (2005) and WILMS & BÖHME (2007).

Distribution: For discussion and map of the distribution range see WILMS & BÖHME (2007).

***Uromastyx ornata philbyi* Parker, 1938**

Uromastyx philbyi Parker, 1938; Ann. Mag. nat. Hist. (11) 1: 484.

Uromastyx ocellatus philbyi – ARNOLD 1986; Fauna of Saudi Arabia 8: 416.

Uromastyx ornatus philbyi – ARNOLD 1987; Proc. Symp. Fauna Zoogeogr. Middle East. 28: 249.

Uromastyx ocellata philbyi – SCHÄTTI & GASPARETTI 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – SCHÄTTI & DESVOIGNES 1999; The Herpetofauna of southern Yemen and the Sokotra Archipelago: 39.

Holotype: BMNH 1946.8.14.65 (former number: BMNH 1938.2.1.1), male, between Makkah and Shabwa, southern Hejaz, between Mountains and Rub al Khali, Saudi Arabia, coll. H. ST. J. B. PHILBY, without date.

Differential diagnosis: see under *U. o. ornata*.

Description: Maximum total length 341 mm, maximum SVL 205 mm (MZUF 27906). 138–193 scales around midbody, 69–96 scales between gular- and inguinal fold, 17–31 gular scales, 18–22 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–5 scales between supralabial and enlarged subocular scale. 22–29 scales around 5th whorl. 17–22 tail whorls. 11–14 scales beneath 4th left toe. 7–14 preanofemoral pores on each side.

Colouration: Similar to *Uromastyx o. ornata*. For pictures of live specimens see WILMS (2007 b).

Distribution: For discussion and map of the distribution areas of this taxon see WILMS & BÖHME (2007).

***Uromastyx ocellata* Lichtenstein, 1823**
[Common name: Eyed Spiny-tailed Lizard]

Uromastyx ocellatus Lichtenstein, 1823; Verz. Doubl. zool. Mus. k. Univ. Berlin: 107.

Uromastix ornatus – BOULENGER 1885; Cat. Liz. Brit. Mus.,1: 406.

Uromastix ocellatus – ANDERSON 1898; Zool. Egypt, 1 Rept. Batr.: 127.

Uromastyx ocellata ocellata – LANZA 1988; Biogeographia 14: 420.

Syntypes: ZMB 809, Nubia; ZMB 811–13, Nubia; ZMB 810, Syria; all specimens leg. Hemprich & Ehrenberg. After DENZER et al. (1997), ZMB 811–13 are lost which we cannot confirm at least for ZMB 811.

Differential diagnosis: *Uromastyx ocellata* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group and *U. macfadyeni*) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. benti*, *U. shobraki* and *U. yemenensis* the species differs in possessing preanofemoralpores and from *U. ornata* and *U. macfadyeni* in lacking enlarged scales on the anterior margin of the ear opening.

Subspecies: None

Description: Maximum total length 276 mm, maximum SVL 174 mm. 189–256 scales around midbody, 95–113 scales between gular- and inguinal fold, 29–42 gular scales, 23–33 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–6 scales between supralabial and enlarged subocular scale. 24–39 scales around 5th whorl. 22–29 tail whorls. 14–19 scales beneath 4th left toe. 12–17 preanofemoral pores on each side.

Colouration: Showing a distinctive sexual dichromatism. Ground colour of males either beautifully red with a black vermiculation, olive green with red dots or red with green dots. On the back 7–8 transversal rows of yellow or white, black edged ocellae. Sides of the neck, throat and breast light green or lively blue coloured. The belly is monochromatic yellow or white. Females are by far not as lively coloured as the males, with an either pale brownish, green, redish or grey groundcolour. For pictures of live specimens see Wilms (2005) and Frahm (2006).

Distribution: This species occures in the dry areas west of the red sea in the following countries: Somalia (Borama district), Djibouti, Eritrea, Sudan and southeastern Egypt, where the southernmost locality is in the Borama district (northwestern Somalia) and the northernmost in the Wadi Gul'an (Egypt). According to Largen & Spawls (2006) this species lives also in Ethiopia near the border to Somalia.

Uromastyx occidentalis Mateo, Geniez, López-Jurado & Bons, 1998
[Common name: Western Giant Spiny-tailed Lizard]

Uromastyx occidentalis Mateo, Geniez, López-Jurado & Bons, 1998

Holotype: DB.ULPGC-5 (Departamento de Biología, Universidad de Las Palmas de Gran Canaria), Aagtel Agmumuit, between Yeloua and Mades (Adrar Souttouf, Western Sahara) (21° 52'N, 15° 31'W), coll. M. Hasi, 25. June 1995.

Differential diagnosis: *U. occidentalis* is distinguished from *U. thomasi* and *U. princeps* by the longer tail; from the species of the *U. ocellata* group and *U. macfadyeni* by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group and *U. macfadyeni*) vs. less than 7 whorls forming a continuous scale row in *U. occidentalis*; from the species of the *U. acanthinura* group by more scales around midbody (297–301 in *U. occidentalis* vs. 142–231 in the species of the *U. acanthinura* group). *U. occidentalis* is distinguished from *U. aegyptia* by lacking preanofemoral pores.

Subspecies: None

Description: Maximum total length 536 mm, maximum SVL 228 mm. 297–301 scales around midbody, 121–122 scales between gular- and inguinal fold. On both sides 7 scales between supralabial and enlarged subocular scale. 23 whorls. No preanofemoral pores.

Colouration: Colouration in life not known. For picture of the holotype see Mateo et al. (1998) and Wilms (2005).

Distribution: Known only from the type locality and from Udei Sfa (45 km west of Maatal Laj, 22°22'N 15°32'W; Geniez et al. 2004).

Uromastyx princeps O'Shaughnessy, 1880
[Common name: Princely Spiny-tailed Lizard]

Uromastix princeps O'Shaughnessy, 1880; Proc. zool. Soc. London, 1880: 445.

Aporoscelis princeps – Boulenger 1885; Cat. Liz. Brit. Mus.,1: 410.

Uromastix princeps scorteccii – Cherchi 1954; Atti. Soc. ital. Sci. Nat. Milano, 93: 540.

Uromastyx princeps – Lanza 1983; Monitore zool. ital. (new Series) Suppl. 18: 208

Uromastyx scortecci – Moody 1987; Proc. 4th General Meeting of the Societas Europaea Herpetologica: 286.

Holotype: BMNH 1946.814.56, male, Zanzibar, coll. Sir J. Kirk, without date (see comments on type locality in Wilms 2001).

Differential diagnosis: With the exception of *Uromastyx thomasi*, *U. princeps* is distinguished from all other taxa in the genus by its significantly shorter tail. From *U. thomasi* it is distinguished by the absence of preanofemoral pores.

Subspecies: None

Description: Maximum total length 265 mm, maximum SVL 180 mm. 150–226 scales around mid–body, 77–128 scales between gular- and inguinal fold, 28–43 gular scales, 22–34 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 2–5 scales between supralabial and enlarged subocular scale. 20–27 scales around 5th whorl. 9–14 tail whorls. 14–18 scales beneath 4th left toe. No preanofemoral pores.

Colouration: This species displays a pronounced sexual dimorphism. The ground colour of the body is olive grey to green with small brown markings. Males have a yellowish red to green dorsum with small, scattered black spots. The venter is yellowish with blue grey marbling in the area of the chest and throat. The tail is yellow green or red in colour. Females are grey brown dorsally with a light red shimmer and small black spots. The venter is immaculate white. For pictures of live specimens see Wilms & Hulbert (1995) and Wilms (2005).

Distribution: *Uromastyx princeps* is found in the Somalian provinces of Sanaag, Bari, Nogal and Mudug.

Uromastyx shobraki **Wilms & Schmitz, 2007 new status**

[Common name: Shobrak's Spiny-tailed Lizard]

Uromastyx ocellata benti – Schätti & Gasparetti 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – Schätti & Desvoignes 1999; The Herpetofauna of southern Yemen and the Sokotra Archipelago: 39.

Uromastyx yemenensis shobraki Wilms & Schmitz, 2007; Zootaxa 1394: 16.

Holotype: ZFMK 48681, adult male, Mafraq Mocca (Mafraq al-Mukha), km 13.5, Republic of Yemen, leg. B. Schätti, 5.–6.IV.1988.

Differential diagnosis: *Uromastyx shobraki* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. ocellata*, *U. ornata* and *U. macfadyeni* the species differs in lacking femoral- and preanal-pores.

Uromastyx shobraki differs from *U. benti* in having smaler scales around midbody (188.92 +/- 13.22 in *U. shobraki* vs. 160.05 +/- 8.98 in *U. benti*) and smaller ventrals (86.64 +/-4.88 in *U. shobraki* vs. 74 +/-4.02 in *U. benti*). *U. shobraki* is differentiated from *U. yemenensis* not only by its larger maximum size (393 mm in *U. shobraki* vs. 337 mm in *U. yemenensis*) but also in different colour pattern and in significant genetic differences.

Subspecies: None

Description: Maximum total length 393 mm, maximum SVL 208 mm. 163–207 scales around midbody, 79–97 scales between gular- and inguinal fold, 25–33 gular scales, 23–31 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 3–5 scales between supralabial and enlarged subocular scale. 32–39 scales around 5th whorl. 24–27 tail whorls. 15–17 scales beneath 4th left toe. No preanofemoral pores.

Colouration: In preserved specimens dorsal surface of head, body and hindlimbs dark brown, tail lighter. Light brown roundish dots (diameter 4–5 scales) are present on the dorsum, tending to form transverse rows. In addition, irregular light brown dots are present on the whole dorsum. Colour of the hands not different to the colour of the forearm. Head dark brown, with light brown pattern. Ventral side yellowish brown. Ventral side of head and chest marbled with anthracite and dark brown. For a picture of a live specimen see Wilms & Böhme (2007).

Distribution: South-western Yemen. For a map of the distribution area see Wilms & Böhme (2007).

Uromastyx thomasi **Parker, 1930**

[Common name: Omani Spiny-tailed Lizard]

Uromastix thomasi Parker, 1930; Ann. Mag. nat. Hist., London, (10) 6: 595.

Uromastyx thomasi – Arnold 1980; J. Oman Stud. Spec. Rep. No. 2: 293.

Holotype: BMNH 1946.8.14.43 (former number: BMNH 1930.6.30.2), male, Bu Ju'ay, Rub al Khali, Dhofar, Oman, coll. B. Thomas, without date.

Differential diagnosis: With the exception of *Uromastyx princeps*, *U. thomasi* is distinguished from all other taxa in the genus by its significantly shorter tail. From *U. princeps* it is distinguished by the presence of preanofemoral pores.

Subspecies: None

Description: Maximum total length approx. 24 cm, maximum SVL approx. 19 cm. 125–150 scales around midbody, 72–100 scales between gular- and inguinal fold, 25–36 gular scales between a hypothetical line between the anterior margins of the ears and the mental scale, 19–25 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 2–4 scales between supralabial and enlarged subocular scale. 28–34 scales around 5th whorl. 11–13 whorls. 13–18 scales beneath 4th left toe. 12–19 preanofemoral pores each side.

Colouration: Yellowish green with a dark net-like pattern. A broad red vertebral-stripe runs from the neck to the first half of the tail. In some specimens an orange to red colouration of the head can occur. Ventral side yellowish or white. Neck and sides of the head of the juveniles striped (black and white). Colouration of the upper side of the body black with 6 lighter transversal bands. Between those bands yellowish to orange coloured ocellae. Tail above brown with some large black spots. Belly and throat white. Ventral side of the tail white with black dots. For pictures of live specimens see Wilms et al. (2002)

Distribution: *Uromastyx thomasi* lives in coastal Oman (for map see Wilms & Böhme 2007).

Uromastyx yemenensis Wilms & Schmitz, 2007 [Common name: South Arabian Spiny-tailed Lizard]

Uromastyx ocellata benti – Schätti & Gasparetti 1994; Fauna of Saudi Arabia 14: 369.

Uromastyx ocellata – Schätti & Desvoignes 1999; The Herpetofauna of southern Yemen andthe Sokotra Archipelago: 39.

Uromastyx y. yemenensis Wilms & Schmitz, 2007; Zootaxa 1394: 12.

Holotype: ZFMK 47861, adult male, Abyan Governorate, vicinity of Lodar (= Lawdar), Republic of Yemen, leg. I. Haikal, don. 1985.

Differential diagnosis: *Uromastyx yemenensis* is distinguished from *U. thomasi* and *U. princeps* by the significantly longer tail. From all remaining species of the genus (with the exception of the *U. ocellata* group) by the arrangement of the annuli of the tail: last 8–21 forming a continuous scale row each (*U. ocellata* group) vs. 2–5 whorls forming a continuous scale row (all other *Uromastyx* species). From *U. ocellata*, *U. ornata* and *U. macfadyeni* the species differs in lacking femoral– and preanalpores.

Uromastyx yemenensis differs from *U. benti* in having smaler scales around midbody (197.44 +/-20.9463 in *U. yemenensis* vs. 160.05 +/- 8.98 in *U. benti*) and smaler ventralia (88.25 +/-6.98 in *U. yemenensis* vs. 74 +/-4.02 in *U. benti*). *U. yemenensis* is differentiated from *U. shobraki* not only by its smaller maximum size (393 mm in *U. shobraki* vs. 337 mm in *U. yemenensis*) but also in different colour pattern and significant genetic differences.

Subspecies: None

Description: Maximum total length 337 mm, maximum SVL 185 mm. 146–227 scales around midbody, 73–100 scales between gular- and inguinal fold, 25–40 gular scales, 22–30 scales counted from the mid of the lower end of the ear opening to the mental scale. On both sides 4–6 scales between supralabial and enlarged subocular scale. 33–40 scales around 5th whorl. 23–27 tail whorls. 12–18 scales beneath 4th left toe. No preanofemoral pores.

Colouration: Ground colour of the males back, tail and hind legs yellowish brown. Tail without distinct pattern, hind legs with very small dark brown dots. Back with a pattern consisting of dark brown lines and dots; five distinct cross bands without or with very few pattern on the back. Dorsal side of the front legs anthracite coloured. Hands yellowish brown. Head yellowish brown, dark brown marbled. Underside of the head anthracite coloured with some yellowish brown dots. Ventral parts of forelegs and chest marbled with grey. Belly with narrow grey/anthracite crossbands. The females are much paler in colouration. With a yellowish brown ground colour with a pattern of small dark brown lines and dots. Five pale cross bands on the back. The ground colour of the ventral side is a light yellowish brown.

Distribution: South-western Yemen. For a map of the distribution area see Wilms & Böhme (2007).

KEY TO THE SPECIES OF THE GENERA *SAARA* GRAY, 1845 AND *UROMASTYX* MERREM, 1820

1 a – Tail whorls separated dorsally by 1–6 continuous rows of intercalary scales..*Saara*

b –Tail whorls without dorsal intercalary scales ....*Uromastyx*

Saara Gray, 1845

1 a –Tail with 29–36 primary whorls; 2–6 rows of keeled intercalary scales between whorls on dorsal surface of tail; dorsal scalation interspersed with irregular, only slightly enlarged, tubercular scales.......................*S. hardwickii*

b –Tail with less than 28 primary whorls; 1–2 rows of unkeeled intercalary scales between tail whorls on dorsal surface of tail; dorsal scalation with transverse rows of conspicuously enlarged tubercular scales 2

2 a – Slightly enlarged scales at front edge of ear opening; 8–13 preanofemoral pores on either side; 7–10 scales in a transverse row on the dorsal surface of the tail base.. *S. asmussi*

b –Without enlarged scales at the front edge of the ear opening; 15–20 preanofemoral pores on either side; 12 scales in a transverse row on the dorsal surface of the tail base..... ....*S. loricata*

***Uromastyx* Merrem, 1820**

1 a – Without preanofemoral pores 2

b – With preanofemoral 6

2 a – Tail short, approx. 35–53 % of SVL; 9–14 whorls ....*U. princeps*

b – Tail long, approx. 71–94 % of SVL; 22–27 whorls 3

3 a – Body scales small, approx. 297–301 scales around midbody; 121–122 scales between gular and inguinal fold .... *U. occidentalis*

b – Body scales larger, approx. 143–227 scales at midbody; 66–100 scales between gular and inguinal fold 4

4 a – 143–187 scales around midbody (average 160.05 +/- 8.98), 66–86 ventral scales ....*U. benti*

b – 163–227 scales around midbody (average 192.53 +/- 16.63), 79–97 ventral scales 5

5 a – Ground colour light brown with five distinct crossbands on the back ....*U. yemenensis*

b – Ground colour dark brown with light brown dots tending to form transverse rows on the back ....*U. shobraki*

6 a – Tail short, approx. 25–35 % of SVL, from above disk-shaped .... *U. thomasi*

b – Tail long, approx. 48–103 % of SVL, from above elongated 7

7 a – The last 12–21 tail whorls formed of continuous scale rows 8

b – The last 2–5 tail whorls formed of continuous scales rows 10

8 a – Anterior margin of ear opening without enlarged scales .... *U. ocellata*

b – Anterior margin of ear opening with enlarged scales 9

9 a – 17–29 (very rarely 31) gular scales; tail width between the 4th and 5th whorl equivalent to 63–79 % of maximum tail width at the 5th whorl .... *U. ornata*

b – 29–32 gulars; tail width between the 4th and 5th whorl equivalent to 56–62 % of maximum tail width at 5th whorl ....*U. macfadyeni*

10a – 238–391 scales at midbody, 112–193 ventrals between gular and inguinal fold .... *U. aegyptia*

b – 138–227 scales at midbody, 68–112 ventrals between gular and inguinal fold 11

11 a – Tail with 20–24 whorls; tail length in adult specimens approx. 70–98 % of SVL 12

b – Tail with 16–21 whorls; tail length approx. 48–75 % of SVL 13

12 a – Several transverse rows of enlarged scales along the flanks; max. total length 35.5 cm; never completely black coloured .... *U. geyri*

b – Flank scalation imbricate with enlarged triangular scales; max. total length 42.9 cm; adult males and occasionally females completely black...........*U. alfredschmidti*

13 a – 79–118 ventrals between gular and inguinal fold; 164–231 scales at midbody; 30–38 scales around 5th whorl .... *U. dispar*

b – 66–99 ventrals between gular and inguinal fold; 139–208 scales at midbody; 25–36 scales form 5th whorl 14

14 a – Adult males black with ivory coloured or yellowish dots, adult females beige to silvergrey with small dark spots.. *U. acanthinura*

b – Colouration very variable, with red, yellow, green and orange coloured specimens. Old adult males show frequently a black colouration of head and belly ....*U. nigriventris*

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Appendix I.

Table 1. Character matrix for thirteen polarized characters (Outgroup *Leiolepis* and all twenty-three taxa in this study). For character coding see Appendix III.

Taxon	A	B	C	D	E	F	G	H	I	J	K	L	M
acanthinura	1	0	0	0	1	0	0	0	0	1	1	0	1
aegyptia	1	0	1	1	1	0	1	0	0	1	0	0	1
alfredschmidti	1	0	0	0	1	0	0	0	0	1	0	0	1
asmussi	1	0	0	0	1	0	0	0	0	2	0	1	0
benti	1	0	0	0	1	0	0	0	1	1	0	0	1
dispar	1	0	0	0	1	0	0	0	0	1	1	0	1
flavifasciata	1	0	0	0	1	0	0	0	0	1	1	0	1
geyri	1	0	0	0	1	0	0	0	0	1	0	0	1
hardwickii	0	0	0	1	0	0	0	0	0	2	0	1	0
leptieni	1	0	1	0	1	0	1	0	0	1	0	0	1
loricata	1	0	0	0	1	0	0	0	0	2	0	1	0
macfadyeni	1	0	0	0	1	0	0	0	1	1	1	0	1
maliensis	1	0	0	0	1	0	0	0	0	1	1	0	1
microlepis	1	0	1	1	1	0	1	0	0	1	0	0	1
nigriventris	1	0	0	0	1	0	0	0	0	1	1	0	1
occidentalis	1	0	1	–	–	–	0	0	0	–	–	0	1
ocellata	1	0	0	0	1	0	0	0	1	1	0	0	1
ornata	1	1	0	0	1	0	0	0	1	1	0	0	1
philbyi	1	1	0	0	1	0	0	0	1	1	1	0	1
princeps	2	0	0	0	1	1	0	1	0	0	2	0	1
shobraki	1	0	0	0	1	0	0	0	1	1	0	0	1
thomasi	2	0	0	0	1	1	0	1	0	0	2	0	1
yemenensis	1	0	0	0	1	0	0	0	1	1	0	0	1
Leiolepis	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 2. List of samples used for genetic analysis (geographic origin, locality and GenBank accession numbers).

Species	Geographic origin	Locality	Voucher	GenBank Accession No.
Tympanocryptis tetraporophora E105.13	Australia	Mount Olga	ZFMK 83840	EF081041 (16s)
Saara asmussi E107.5	Iran	30 km north of Bampur, direction to Zahedan (Pakistan)	NMP6V 73519	FJ639585 (16s)
Saara loricata E107.3	Iran	Chahak, approx. 15 km north of Bandar-e-Genaveh, Province Busheer	ZFMK 87396	FJ639586 (16s)
Saara hardwickii E111.17	unknown	unknown	ZFMK 83797	FJ639587 (16s)
Saara hardwickii E111.18	unknown	unknown	ZFMK 83795	FJ639588 (16s)
Saara hardwickii E111.19	unknown	unknown	ZFMK 83794	FJ639589 (16s)
Saara hardwickii E111.20	unknown	unknown	ZFMK 83796	FJ639590 (16s)
Saara hardwickii E112.2	unknown	unknown	No Voucher	FJ639591 (16s)
Uromastyx acanthinura E105.21	Tunesia	unknown	ZFMK 83816	FJ639630 (12s) FJ639592 (16s)
Uromastyx acanthinura E105.22	Tunesia	unknown	ZFMK 83817	FJ639631 (12s) FJ639593 (16s)
Uromastyx acanthinura E105.23	Tunesia	unknown	ZFMK 83818	FJ639632 (12s) FJ639594 (16s)
Uromastyx acanthinura E107.15	Tunesia	unknown	No Voucher	FJ639633 (12s) FJ639595 (16s)
Uromastyx nigriventris E106.4	Morocco	unknown	ZFMK 83820	FJ639634 (12s) FJ639596 (16s)
Uromastyx nigriventris E106.5	Morocco	Guelmim	ZFMK 83819	FJ639635 (12s) FJ639597 (16s)
Uromastyx nigriventris E107.14	Morocco	Guelmim	ZFMK 84438	FJ639636 (12s) FJ639598 (16s)
Uromastyx dispar dispar E106.2	Chad	Zouar, Tibesti Mountains	ZFMK 84800	FJ639637 (12s) FJ639599 (16s)
Uromastyx dispar dispar E110.19	Chad	Zouar, Tibesti Mountains	ZFMK 84437	FJ639638 (12s) FJ639600 (16s)
Uromastyx dispar flavifasciata E105.15	Mauritania	Captive bred; father from vicinity of Atar, mother from vicinity of Akjoujt	ZFMK 85163	FJ639639 (12s) FJ639605 (16s)
Uromastyx dispar flavifasciata E105.27	Mauritania	Captive bred; father from vicinity of Atar, mother from vicinity of Akjoujt	ZFMK 83824	FJ639640 (12s) FJ639601 (16s)
Uromastyx dispar flavifasciata E106.22	Mauritania	Atar	ZFMK 73500	FJ639641 (12s) FJ639602 (16s)
Uromastyx dispar flavifasciata E110.8	Algeria	Tindouf	ZFMK 84261	FJ639642 (12s) FJ639603 (16s)
Uromastyx dispar flavifasciata E110.9	Algeria	Tindouf	ZFMK 84262	FJ639643 (12s) FJ639604 (16s)
Uromastyx dispar flavifasciata (*obscura*- phenotype) E111.21	Mauritania	Vicinity of Atar	ZFMK 86473	FJ639644 (12s) FJ639606 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E111.22	Mauritania	northern Mauritania	ZFMK 86474	FJ639645 (12s) FJ639610 (16s)
Uromastyx dispar flavifasciata (*obscura*- phenotype) E133.2	Mauritania	33 km southwest of Choum, (21.0036°N/13.1347°W)	No Voucher	FJ639648 (12s) FJ639607 (16s)

Species	Geographic origin	Locality	Voucher	GenBank Accession No.
Uromastyx dispar flavifasciata (*obscura*- phenotype) E133.3	Mauritania	Track Aghmakoum - El Beyed (21°28’23” N/11° 33’ 24” W)	No Voucher	FJ639649 (12s) FJ639608 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.6	Mauritania	south of Choum at 21.0027°N/13.1636°W	No Voucher	FJ639650 (12s) FJ639612 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.7	Mauritania	south of Choum at 21.0027°N/13.1636°W	No Voucher	FJ639651 (12s) FJ639613 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.8	Mauritania	33 km southwest of Choum (21.0043°N/13.1324°W)	No Voucher	FJ639652 (12s) FJ639614 (16s)
Uromastyx dispar flavifasciata (*obscura*- phenotype) E133.9	Mauritania	26 km northwest of Atar (20.7462°N/13.1293°W)	No Voucher	FJ639653 (12s) FJ639609 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.10	Mauritania	track Atar - Choum (21.0003°N / 13.1598°W)	No Voucher	FJ639646 (12s) FJ639615 (16s)
Uromastyx dispar flavifasciata (*obscura*-phenotype) E133.11	Mauritania	26 km northwest of Atar (20.7432°N/13.1183°W)	No Voucher	FJ639647 (12s) FJ639611 (16s)
Uromastyx dispar maliensis E106.26	Mali	unknown	ZFMK 71647	FJ639616 (16s)
Uromastyx geyri E105.24	Niger	Kafadek, near Agadez	ZFMK 83821	FJ639654 (12s) FJ639617 (16s)
Uromastyx geyri E105.25	Niger	Kafadek, near Agadez	ZFMK 83822	FJ639655 (12s) FJ639618 (16s)
Uromastyx aegyptia aegyptia E106.21	Egypt	Sinai Peninsula	ZFMK 83792	FJ639656 (12s) FJ639619 (16s)
Uromastyx aegyptia microlepis E117.7	Saudi Arabia	Mahazat as Sayd	ZFMK 86573	FJ639658 (12s) FJ639620 (16s)
Uromastyx aegyptia microlepis E117.11	Saudi Arabia	Mahazat as Sayd	ZFMK 86567	FJ639657 (12s) FJ639621 (16s)
Uromastyx aegyptia leptieni E106.27	United Arab Emirates	Rimah / Al-Kaznah	No Voucher	FJ639659 (12s) FJ639622 (16s)
Uromastyx aegyptia leptieni E.110.14	United Arab Emirates	Wadi Siji	ZFMK 52398 Holotype	FJ639660 (12s) FJ639623 (16s)
Uromastyx benti E106.3	Oman	Dhofar, vicinity of Mirbat	ZFMK 83801	EF081054 (16s)
Uromastyx benti E111.2	Oman	Dhofar, vicinity of Mirbat	ZFMK 73681	EF081055 (16s)
Uromastyx benti E111.4	Oman	Dhofar, vicinity of Mirbat	ZFMK 83347	EF081056 (16s)
Uromastyx benti E111.13	Oman	Dhofar, vicinity of Mirbat	ZFMK 73680	EF081057 (16s)
Uromastyx yemenensis E111.12	Yemen	Abian, southern Yemen	ZFMK 47861 Holotype	EF081058 (16s)
Uromastyx yemenensis E106.18	Yemen	unknown	ZFMK 83805	EF081059 (16s)
Uromastyx yemenensis E106.19	Yemen	unknown	ZFMK 83806	EF081060 (16s)
Uromastyx yemenensis E106.20	Yemen	unknown	ZFMK 83807	EF081061 (16s)
Uromastyx shobraki E111.1	Yemen	Mocca, northern Yemen	ZFMK 73677	EF081065 (16s)
Uromastyx shobraki E111.3	Yemen	Mocca, northern Yemen	ZFMK 73676	EF081066 (16s)
Uromastyx shobraki E111.6	Yemen	Between Mafraq and Mocca, northern Yemen	ZFMK 48681 Holotype	EF081067 (16s)
Uromastyx shobraki E111.7	Yemen	Mocca, northern Yemen	ZFMK 73675	EF081068 (16s)
Uromastyx macfadyeni E112.1	Somalia	unknown	ZFMK 84441	EF081042 (16s)

Species	Geographic origin	Locality	Voucher	GenBank Accession No.
Uromastyx macfadyeni E112.3	Somalia	unknown	ZFMK 84440	EF081043 (16s)
Uromastyx ocellata E106.6	Sudan	unknown	ZFMK 83798	EF081044 (16s)
Uromastyx ocellata E106.7	Sudan	unknown	ZFMK 83799	EF081045 (16s)
Uromastyx ornata ornata E106.11	Egypt	Sinai Peninsula	ZFMK 83815	EF081051 (16s)
Uromastyx ornata ornata E106.8	Egypt	Sinai Peninsula	ZFMK 83812	FJ639629 (12s) EF081052 (16s)
Uromastyx ornata ornata E106.9	Egypt	Sinai Peninsula	ZFMK 83813	EF081053 (16s)
Uromastyx ornata philbyi E110.20	Saudi Arabia	19°05'N 41°50'E, Tihama	ZFMK 84442	EF081046 (16s)
Uromastyx princeps E106.24	Somalia	Bossasso	ZFMK 58985	FJ639624 (16s)
Uromastyx princeps E106.25	Somalia	Bossasso	ZFMK 58048	FJ639625 (16s)
Uromastyx thomasi E105.4	Oman	Vicinity of Ras Hilf, Masirah Island	ZFMK 83830	FJ639626 (16s)
Uromastyx thomasi E105.11	Oman	Vicinity of Ras Hilf, Masirah Island	ZFMK 83837	FJ639627 (16s)
Uromastyx thomasi E105.12	Oman	Vicinity of Ras Hilf, Masirah Island	ZFMK 83838	FJ639628 (16s)

Table 3. Variables used to calculate the distance phenogram (Fig. 3); for definition of appreviations see "Material and Methods".

Variable	**V1**	**V2**	**V3**	**V4**	**V5**	**V6**	**V7**	**V8**	**V9**
Definition	W	SD	G	MBS	V	SW	PP left	PP right	LS left
Variable	**V10**	**V11**	**V12**	**V13**	**V14**	**V15**	**V16**	**V17**	**V18**
Definition	LS right	SO left	SO right	HS left	HS right	ES * PES	IS	TF	TD

Table 4. Definition of variables used for the PCA separating OTU I and OTU II; for definition of abbreviations see "Material and Methods".

Variable	**V1**	**V2**	**V3**	**V4**	**V5**	**V6**	**V7**	**V8**	**V9**
Definition	W	SD	G	MBS	V	SW	PP left	PP right	LS left
Variable	**V10**	**V11**	**V12**	**V13**	**V14**	**V15**	**V16**	**V17**	
Definition	LS right	SO left	SO right	HS left	HS right	ES * PES	IS	TD	

Table 5. Factor loading on the first four principal components (PC) from a correlation matrix of V1–V17 for individuals of OTU I and OTU II.

Variable	PC 1	PC 2	PC 3	PC 4
V1	- 0.066	0.293	- 0.092	0.073
V2	0.189	- 0.062	- 0.159	0.041
V3	0.194	- 0.147	0.089	- 0.040
V4	0.199	- 0.092	- 0.009	- 0.050
V5	0.176	- 0.066	0.021	- 0.031
V6	0.022	0.205	- 0.133	0.157
V7	- 0.050	- 0.021	0.456	- 0.017
V8	- 0.050	- 0.018	0.458	- 0.027
V9	- 0.033	0.022	- 0.031	0.462
V10	- 0.035	0.029	- 0.014	0.458
V11	0.045	0.131	0.017	0.022
V12	0.064	0.115	- 0.011	0.050
V13	0.162	- 0.035	0.016	- 0.023
V14	0.167	- 0.050	0.022	- 0.026
V15	0.129	0.068	- 0.153	- 0.042
V16	- 0.116	0.324	0.033	- 0.016
V17	- 0.128	0.264	0.166	- 0.206
Eigenvalues	7,264	2,512	1,959	1,560
Accumulated percent of trace	42,731	57,508	69,031	78,207

Table 6. Definition of variables used for the PCA separating species and species groups within *Uromastyx* (Figs 5–10); for definition of abbreviations see "Material and Methods".

Variable	**V1**	**V2**	**V3**	**V4**	**V5**	**V6**	**V7**	
Definition	W	SD	G	MBS	V	SW	PP left	
Variable	**V8**	**V9**	**V10**	**V11**	**V12**	**V13**	**V14**	**V15**
Definition	PP right	LS left	LS right	SO left	SO right	HS left	HS right	ES * PES

Table 7. Factor loading on the first four principal components (PC) from a correlation matrix of V1–V15 for 431 individuals of *Uromastyx*.

Variable	**PC 1**	**PC 2**	**PC 3**	**PC 4**	**PC 5**
V1	0.274	- 0.216	0.598	0.246	0.581
V2	0.630	- 0.311	- 0.265	0.433	- 1.898E-02
V3	0.850	7.232E-02	- 0.219	9.518E-02	- 0.168
V4	0.841	- 0.148	- 0.133	0.346	7.417E-02
V5	0.824	- 6.121E-02	- 0.234	0.365	2.631E-02
V6	0.622	- 0.105	0.475	0.148	9.023E-02
V7	0.433	0.715	- 0.314	- 0.134	0.403
V8	0.439	0.702	- 0.316	- 0.137	0.419
V9	0.147	0.753	0.402	0.261	- 0.295
V10	0.166	0.785	0.358	0.239	- 0.288
V11	0.742	-2.223E-02	0.308	- 0.430	8.690E-02
V12	0.755	-1.883E-02	0.281	- 0.439	- 4.109E-02
V13	0.857	- 5.430E-02	- 8.995E-02	- 0.220	- 0.253
V14	0.852	- 3.638E-02	- 9.704E-02	- 0.200	- 0.273
V15	0.649	- 0.488	0.115	- 8.413E-02	6.694E-03
Eigenvalues	6.399	2.615	1.466	1.166	1.037
Accumulated percent of trace	42.662	60.097	69.870	77.646	84.560

Table 8. Factor loading on the first three principal components (PC) from a correlation matrix of V1–V15 for 354 individuals of *Uromastyx*.

Variable	**PC 1**	**PC 2**	**PC 3**
V1	0.337	- 0.403	- 0.427
V2	0.728	- 5.468E-02	- 0.354
V3	0.884	0.147	1.143E-02
V4	0.872	- 2.405E-02	- 0.240
V5	0.860	4.975E-02	- 0.246
V6	0.757	0.105	2.198E-02
V7	0.603	0.500	- 0.418
V8	0.611	0.442	- 0.446
V9	6.418E-02	0.831	0.311
V10	7.056E-02	0.835	0.323
V11	0.715	- 0.282	0.449
V12	0.724	- 0.228	0.504
V13	0.848	- 7.847E-02	0.314
V14	0.852	-4.002E-02	0.308
V15	0.715	- 0.381	8.754E-02
Eigenvalues	7.238	2.318	1.658
Accumulated percent of trace	48.250	63.706	74.756

Table 9. Factor loading on the first four principal components (PC) from a correlation matrix of V1–V15 for 331 individuals of *Uromastyx*.

Variable	PC 1	PC 2	PC 3	PC 4
V1	0.363	0.221	4.585E-02	0.809
V2	0.727	0.130	- 0.320	0.144
V3	0.894	5.650E-02	- 1.491E-02	- 6.992E-02
V4	0.874	0.117	- 0.139	0.289
V5	0.861	0.150	- 0.167	0.235
V6	0.765	- 1.862E-02	- 0.121	- 0.329
V7	0.630	0.532	- 0.327	- 0.247
V8	0.626	0.520	- 0.335	- 0.256
V9	0.193	0.607	0.664	- 5.942E-02
V10	0.211	0.599	0.653	- 6.505E-02
V11	0.711	- 0.462	0.288	- 6.479E-03
V12	0.724	- 0.496	0.260	- 3.671E-02
V13	0.850	- 0.282	0.130	- 0.121
V14	0.855	- 0.245	0.146	- 0.104
V15	0.749	- 0.280	0.145	3.519E-02
Eigenvalues	7.463	2.064	1.462	1.089
Accumulated percent of trace	49.751	63.512	73.262	80.523

Table 10. Factor loading on the first three principal components (PC) from a correlation matrix of V1–V7 & V10–V15 for 317 individuals of *Uromastyx* (because V8 & V9 are coding for preanofemorapores, it is justified to exclude these variables in the PCAs dealing exclusively with species possessing preanofemoralpores).

Variable	PC 1	PC 2	PC 3
V1	0.271	0.620	- 0.564
V2	0.766	0.213	- 0.369
V3	0.879	9.939E-02	1.397E-02
V4	0.852	0.249	- 0.281
V5	0.849	0.265	- 0.270
V6	0.786	- 5.101E-02	4.997E-02
V7	0.137	0.684	0.601
V10	0.162	0.695	0.581
V11	0.751	- 0.359	0.234
V12	0.764	- 0.406	0.226
V13	0.870	- 0.202	0.148
V14	0.873	- 0.161	0.158
V15	0.768	- 0.164	8.008E-02
Eigenvalues	6.799	1.912	1.468
Accumulated percent of trace	52.301	67.010	78.299

Table 11. Factor loading on the first three principal components (PC) from a correlation matrix of V1–V7 & V10–V15 for 265 individuals of *Uromastyx* (because V8 & V9 are coding for preanofemorapores, it is justified to exclude these variables in the PCAs dealing exclusively with species possessing preanofemoralpores).

Variable	PC 1	PC 2	PC 3
V1	- 0.289	0.578	- 0.458
V2	0.486	0.328	- 0.502
V3	0.774	0.190	0.127
V4	0.677	0.310	- 0.328
V5	0.704	0.352	- 0.309
V6	0.757	0.151	4.432E-02
V7	- 5.536E-02	0.618	0.619
V10	- 3.002E-02	0.684	0.576
V11	0.716	- 0.397	0.239
V12	0.764	- 0.384	0.210
V13	0.895	- 2.617E-02	9.960E-02
V14	0.890	1.378E-02	0.130
V15	0.747	- 8.992E-02	- 8.770E-02
Eigenvalues	5.694	1.884	1.534
Accumulated percent of trace	43.804	58.295	70.092

Table 12. Factor loading on the first three principal components (PC) from a correlation matrix of V1–V7 & V10–V15 for 223 individuals of *Uromastyx* (because V8 & V9 are coding for preanofemorapore, it is justified to exclude these variables in the PCAs dealing exclusively with species possessing preanofemoralpores).

Variable	PC 1	PC 2	PC 3
V1	- 0.554	0.490	- 0.118
V2	- 9.640E-02	0.494	- 0.325
V3	0.743	0.315	- 0.112
V4	0.396	0.515	- 0.282
V5	0.417	0.529	- 0.308
V6	0.662	0.239	- 4.877E-02
V7	0.140	0.497	0.741
V10	0.110	0.580	0.680
V11	0.656	- 0.491	0.209
V12	0.707	- 0.495	0.147
V13	0.866	4.393E-02	- 0.100
V14	0.876	8.752E-02	- 9.225E-02
V15	0.563	- 0.131	1.228E-02
Eigenvalues	4.434	2.283	1.405
Accumulated percent of trace	34.108	51.667	62.473

Appendix II.

List of examined specimens

Saara asmussi (Strauch, 1863)

MHNP 1989.3005, unknown; ZFMK 7925, Afghanistan, Seistan, 50 km east Seranj; BMNH 1964.279, Pakistan, Kharan / Balutschistan; BMNH 74.11.239, Iran, near Rigan / Narmashir; BMNH 79.8.15.18, Afghanistan, Ghorak; BMNH 79.8.15.30, Afghanistan, Ghorak.

Saara hardwickii (Gray, 1827)

NMW 21175, Pakistan, Sindh; NMW 21167:1, India, Katchh; NMW 21167:2, India, Katch; NMW 21167:3, India Katchh; NMW 21173, unknown, foothills of the western Himalaya; NMW 21169:1, Pakistan, Sindh; NMW 21169:2, Pakistan, Sindh; NMW 21169:3, Pakistan, Sindh; NMW 15121:2, India, Katchh; NMW 19981:2, Pakistan, Karachi; NMW 19981:3, Pakistan, Karachi; NMW 19981:4, Pakistan, Karachi; NMW 19981:5, Pakistan, Karachi; MHNP 1962.726, Pakistan, Gizri; MHNP 1962.727, Pakistan, Gizri; MHNP 1962.728, Pakistan, Gizri; ZSM 327/79, Pakistan, Uthal; ZSM 20/1912, Pakistan, Habb; ZSM 7/1912, Pakistan, Wajara; ZSM 7/1912, Pakistan, Wajara; ZFMK 21453, Pakistan, Mokran coast; ZFMK 8616, Afghanistan, Nimla to Djalalabad; ZFMK 21454, Pakistan, Mokran coast; ZFMK 21455, Pakistan, Mokran coast; ZFMK 22103, Pakistan, Mokran coast; BMNH 1933.4.1.23, India, Thar Parkar/Rajputana; BMNH 1933.4.1.24, India, Thar Parkar/Rajputana; BMNH 91.9.11.9, Pakistan, Sindh; BMNH 60.3.19.1006, India, Goojerat; BMNH 1973.447, Pakistan, Karachi; BMNH 1946.8.14.44, India, Plains of Kanouge/Hindustan; BMNH 98.12.22.10, Pakistan, Karachi.

Saara loricata (Blanford, 1874)

NMW 21177, Iran, Bushir; NMW 21179:1, Iran, Bushir; NMW 21179:2, Iran, Bushir; ZSM 2/1966, Iraq, Chankin / southeast Bagdad; ZFMK 22072, Iran, Ahwaz; ZFMK 44906, Iraq, Kirkuk; ZFMK 40594, Iraq, Kirkuk; ZFMK 40593, Iraq, Kirkuk; ZFMK 40592, Iraq, Kirkuk; ZFMK 40591, Iraq, Kirkuk; ZFMK 40590, Iraq, Kirkuk; BMNH 1933.4.1.25, Iran, Bushir; BMNH 87.9.22.19, Iran, Bushir; BMNH 1905.10.14.21, Iran, 30 mls northwest Ahwaz.

Uromastyx acanthinura Bell, 1825

BMNH 1907.4.6.14, Algeria, Biskra; BMNH 1907.4.6.15, Algeria, Biskra; BMNH 1912.11.9.4.6., Algeria, Fort Miribel; BMNH 1912.11.9.50, Paratype of *Uromastix acanthinurus nigerrimus*, Algeria, Oued Mya; BMNH 1912.11.9.51, Paratype of *Uromastix acanthinurus nigerrimus*, Algeria, Ain Guettara; BMNH 1938.7.5.10, Algeria, Biskra; BMNH 1938.7.5.11, Algeria, Bistra; BMNH 1938.7.5.12, Algeria, Bistra; BMNH 1938.7.5.13, Algeria, Biskra; BMNH 1964.2075, Libya, Ain Uif Jebel Nefrousa; BMNH 1969.2088, Algeria, Bistra; BMNH 1969.2090, Algeria, Bistra; BMNH 1969.2091, Algeria, Bistra; BMNH 1969.2106, Algeria, Touggourt; BMNH 1969.2107, Algeria, Touggourt; BMNH 1969.2108, Algeria, Touggourt; BMNH 71.4.16.52, Algeria, Bistra; BMNH 91.4.5.41, Algeria, Bistra; BMNH 91.4.5.42, Algeria, Biskra; BMNH 91.5.439, Tunesia, Duirat; BMNH 91.5.440, Tunesia, Duirat; BMNH 96.2.29.1, Tunesia; Duirat; MZUF 13757, Algeria, Touggourt (Tourghuf); MZUF 21666, Somalia, unreliable locality!; MZUF 25125, Tunesia, Tamerza/Gafsa; MZUF 25126, Tunesia, Tamerza/Gafsa; MZUF 743, Libya, Bu Ngem; MZUF 744, Libya, Cirenaica (Barqa), NMW 21192:1, Tunesia, Gafsa; NMW 21192:2, Tunesia, Gafsa; NMW 21192:3, Tunesia, Gafsa; NMW 21197:1, Algeria, Bistra; NMW 21198:1, Tunesia, Gafsa; NMW 21198:10, Tunesia, Gafsa; NMW 21198:2, Tunesia, Gafsa; NMW 21198:3, Tunesia, Gafsa; NMW 21198:4, Tunesia, Gafsa; NMW 21198:5, Tunesia, Gafsa; NMW 21198:6, Tunesia, Gafsa; NMW 21198:7, Tunesia, Gafsa; NMW 21198:8, Tunesia, Gafsa; NMW 21198:9, Tunesia, Gafsa; NMW 21202:1, Algeria, Biskra; NMW 21202:2, Algeria, Bistra; NMW 21207, Tunesia, Gafsa; NMW 21208, Tunesia, El Guietar; NMW 22116, Libya, Tripolis; SMNS 602:1, Algeria, Biskra; ZFMK 2707, Tunesia, Gabes (Quderef); ZFMK 2708, Tunesia, Gabes-Matmata; ZFMK 2709, Algeria, Biskra; ZFMK 2710, Algeria, Biskra; ZFMK 2711, Algeria, Biskra; ZFMK 2714, Algeria, Biskra; ZMH-R4507, Algeria, Biskra; ZMH-R4508, Algeria, Biskra; ZMH-R4509, Algeria, Biskra; ZSM 112/1983, Libya, south of Tripolis; ZSM 18/1968 (1), Libya, Jebel el Soda; ZSM 18/1968 (2), Libya, Jebel el Soda; ZSM 18/1968 (3), Libya, Jebel el Soda; ZSM 18/1968 (4), Libya, Jebel el Soda; ZSM 181/36, Libya, Jebel el Soda; ZSM 26/1951 (1), Tunesia, Nefta south of Tozeur; ZSM 26/1951 (2), Tunesia, Nefta south of Tozeur; ZSM 4/1963, Tunesia, El Hamma; ZSM 472/79, Libya, Gharian/Tripolis; ZSM 510/1978, Libya, Wadi Bundindin.

Uromastyx aegyptia

Uromastyx aegyptia aegyptia Forsskål, 1775

BMNH 1908.6.9.6, Egypt, Tor / Sinai; BMNH 1951.1.2.55, Israel, Wadi Araba; BMNH 97.10.28.212, Egypt, Suez; BMNH 97.10.28.213, Egypt, Beltim Delta; MZUF 28899, Saudi Arabia, Sawawin; NMW 21182:1, Egypt, Cairo; NMW 21182:2, Egypt, Desert near Cairo; NMW 21183, Egypt, Suez; NMW 21187, Egypt, Cairo; NMW 21222, Egypt, Beltim; ZFMK 2703, Egypt, Lower Egypt; ZFMK 2704, Egypt, Lower Egypt; ZFMK 39073, Egypt, Suez; ZFMK 44216, Neotype of *Uromastyx aegyptia aegyptia*, Egypt, Suez; ZFMK 46502, Egypt; ZFMK 46504, Egypt; ZFMK 64405, Egypt, vicinity of Hurgharda; ZFMK 64406, Jordan, Wadi Araba.

Uromastyx aegyptia microlepis Blanford, 1874

BMNH 1930.6.30.3, Yemen, Bin Khautar / Hadramaut; BMNH 1946.8.11.67, Iraq, Paralectotype of *Uromastyx microlepis*, Basrah; BMNH 1946.8.14.55, Lectotype of Uromastyx microlepis, Iraq, Basrah; BMNH 1950.1.4.71, Oman; BMNH 1950.1.5.4, Arabia, Miofa; BMNH 1952.1.3.51, Saudi Arabia, ElGaisuma-Turaif; BMNH 1953.1.8.50, Yemen, North of Jol / Hadramaut; BMNH 1970.2076; Saudi Arabia, Ruma; BMNH 1970.2481, Bahrain, Ras Al Barr; BMNH 1970.2482, Bahrain, Ras Al Barr; BMNH 1971.748, Bahrain; BMNH 1972.1259, United Arab Emirates, Al Hamran / Abu Dhabi; BMNH 1972.833, United Arab Emirates, near Bada Zaid / Abu Dhabi; BMNH 1978.2072, Kuwait; BMNH 1980.569, Oman, Jiddat al Harasis; BMNH 1982.1327, Saudi Arabia, Dib Dibah; BMNH 1982.1328, Saudi Arabia, Dib Dibah; BMNH 1985.880, Saudi Arabia, 30 km SE Ronya; BMNH 1986.435, Saudi Arabia, Shigree; BMNH 1988.214, Saudi Arabia, 26°56'N, 38°59'E; BMNH 1988.93, Saudi Arabia, Al Rawdah, north of Khobar; BMNH 1996.207, United Arab Emirates, Jebel Gaddah near Jebel Dannah; BMNH 85.7.11.11, Iraq, Fao; BMNH 88.12.6.8, Iraq, Fao; ZFMK 20267, Iraq, Basrah; ZFMK 21091, Iraq, Basrah; ZFMK 42413, Oman, 100 km from Muscat; ZFMK 42414, Oman, 100 km from Muscat; ZFMK 43648, Saudi Arabia, 100 km NO Riyadh; ZFMK 43649, Saudi Arabia, 100 km NO Riyadh; ZFMK 44907, Iraq, Kirkuk; ZFMK 44908, Iraq, Kirkuk; ZFMK 44909, Iraq, Kirkuk; ZFMK 44910, Iraq, Kirkuk; ZFMK 44911, Iraq, Kirkuk.

Uromastyx aegyptia leptieni Wilms & Böhme, 2000

BMNH 1973.2039, United Arab Emirates, S Jebel Jayah; BMNH 1973.2040, United Arab Emirates, Jebel Ali SW Dubai; BMNH 1973.2041, United Arab Emirates, Tawi Bil Khabis 25km WSW Dayd; BMNH 1973.721, Oman, Munay; BMNH 1975.958, Oman, Rostaq 23°24'N 57°27'E; BMNH 85.II.7.4, Oman, Muscat; BMNH 85.II.7.5, Oman, Muscat; ZFMK 52398, Holotype *Uromastyx leptieni*, Wadi Siji.

Uromastyx alfredschmidti Wilms & Böhme, 2001

MHNG 1515.77, Paratype of *Uromastyx alfredschmidti*, Algeria, Tassili n'Ajjers; MHNP 1961.261, Paratype of *Uromastyx alfredschmidti*, Algeria, Hoggar; MHNP 9905, Paratype of *Uromastyx alfredschmidti*, Algeria, Hoggar; NMW 8224:3, Paratype of *Uromastyx alfredschmidti*, Sahara; ZFMK 24643, Holotype of *Uromastyx alfredschmidti*, Algeria, Tassili n'Ajjers /30 km NO Djanet.

Uromastyx benti (Anderson, 1894)

BMNH 1946.8.11.69, Paralectotype of *Uromastyx benti*, Yemen, Makulla, Hadramaut; BMNH 1946.8.11.70, Paralectotype of *Uromastyx benti*, Yemen, Makulla, Hadramaut; BMNH 1946.8.11.71, Paralectotype of *Uromastyx benti*, Yemen, Makulla, Hadramaut; BMNH 1946.8.11.72, Lectotype of *U. benti*, Yemen, Makulla, Hadramaut; BMNH 1953.1.8.52, Yemen, Hadramaut; BMNH 1956.1.7.26, Yemen, Wadi Abr/ Hadramaut; MHNP 1895.43, Paralectotype of *Uromastyx benti*, Yemen, Makulla, Hadramaut; MTKD 24589, Yemen, Makulla; NMW 16174, Yemen, Makulla; NMW 21213:1, Yemen, Makulla; NMW 21213:2, Yemen, Makulla; NMW 21213:3, Yemen, Makulla; NMW 21213:4, Yemen, Makulla; NMW 21213:5, Yemen, Makulla; NMW 21213:6, Yemen, Makulla; NMW 21213:7, Yemen, Makulla; NMW 21213:8, Yemen, Makulla; NMW 21213:9,Yemen, Makulla; NMW 21214:1, Syntype *Uromastyx simonyi*, Yemen, Assan; NMW 21214:2, Syntype *Uromastyx simonyi*, Yemen, Assan; ZFMK 73680, Oman, Mirbat; ZFMK 73681, Oman, Mirbat; ZFMK 83347, Oman, Mirbat; ZFMK 83801, Oman, Mirbat; ZMH R04513, Yemen, Makulla/Hadramaut.

Uromastyx dispar

Uromastyx dispar dispar Heyden, 1827

BMNH 1900.9.12.1, Sudan, Wadi Halfa; BMNH 1913.9.16.15, Sudan, Dongola Provinz; BMNH 1954.1.6.9, Tchad, Tibesti; BMNH 1956.1.1.6, Tchad, S of Zouar; BMNH 1958. 1.3.95, Tchad, Central Tibesti; BMNH 1962.286, Tchad, Bardai; BMNH 1962.287, Tchad, Bardai; BMNH 1973.3348, Tchad, Central Tibesti; BMNH 1986.721, Tchad, Ounianga 19°4'N/20°36'E; GMNH 1952-9100(1), Tchad, Tibesti; GMNH 1952-9100(2), Tchad, Tibesti; MHNP 1974.328, Egypt, Ismailia; MNHP 1993.0692, Tchad, Tibesti; BMNH 1900.9.12.1, Sudan, Wadi Halfa; BMNH 1913.9.16.15, Sudan, Wadi Halfa; SMF10417, Lectotype of *Uromastyx dispar*, Desert near Ambukol; ZFMK 2706, Tchad, Fada; ZFMK 39900, Sudan, SE Debba direction of Khartoum; ZFMK 65600, Tchad, Zouar; ZFMK 65601, Tchad, Zouar; ZFMK 65602, Tchad, Zouar.

Uromastyx dispar flavifasciata Mertens, 1962

BMNH 1969.476, Mauritania, Ouadane; BMNH 1969.477, Mauritania, Ouadane; MHNG 1515.74, Mauritania, Guelta Zemour/Rio de Oro; MHNG 1515.75, Mauritania, Chingetti; MHNG 1515.76, Mauritania, Bir Moghrein/Fort Tringuet; MHNP 1981.178, Mauritania, Richat, Adrar; MHNP 1986.2012, Algeria, Tindouf; MHNP 1993.1501, Mauritania, Atar, Ar bou M'rait; MNHP 1993.5808, Mauritania, Matmata; SMF 58032, Holotype of *Uromastyx acanthinurus flavifasciatus*, Mauritania; ZFMK 17597, Mauritania, Hamdoun; ZFMK 17598, Mauritania, Atar.

Uromastyx dispar maliensis Joger & Lambert, 1996

BMNH 1933.11.18.1, Mali, Gao; BMNH 1933.11.18.2, Mali, Gao; BMNH 1934.1.1.1, Mali, Taberreshat/17°40'N/0°10'E; GNHM 1930.32-5744 RE1772, Paratype *Uromastyx maliensis*, Mali Ti-N-Zaouatene; HLMD RA 1545, Holotype *Uromastyx maliensis*, Mali 40km SE Gao; MHNP 1965.0144, Paratype *Uromastyx maliensis*, Algeria, Taoudrart/Hoggar; NMW 21211, Algeria, Tamanrasset; ZFMK 9232, Algeria, Ahaggar/Gara Djenoun; ZMH-R04529, Algeria, Tassili du Hoggar; 11 Specimens from the trade (Mali).

Uromastyx geyri Müller, 1922

BMNH 1961.417, Niger, near Abangharit/Air; BMNH 1970.1755, Niger, Iferouhane/Air; BMNH 1978.2093, Algeria, Hoggar; BMNH 1978.2094, Algeria, Hoggar; BMNH 1979.402, Algeria, 15km ENE Tamanrasset 22°57'N/05°47'E; BMNH 1986.733, Niger, N of Agadez; MZUF 21013, Algeria, Tamanrasset; MZUF 21014, Algeria, Tamanrasset; MZUF 21015, Algeria, Tamanrasset; MZUF 21017, Algeria, In Ecker 180km N Tamanrasset; GNMH 1930.32-5744 Re1761; MHNG 1513.40, Niger, Tin Teloust/Air; MHNP 1932.128, Algeria, Tanezrouft; MHNP 1943.3, Algeria, Hoggar; MHNP 1974.1412, Algeria, Tefedest; MHNP 1990.4665, Niger, El Meki/Air; MNHP 8971, Niger, Telouess Tabelot; MNHP 8972, Niger, Telouess Tabelot; MTKD 25699, Niger, Agadez; MTKD 25700, Niger, Agadez; SMF 68765, Niger; SMF 68766, Niger; SMF 68767, Niger; ZFMK 9228, Algeria, Ahaggar/In Kelmet; NMW 21210, Algeria, Tamanrasset; NMW 21211, Algeria, Tamanrasset; NMW 22000, Algeria, Hoggar/Tamanrasset; NMW 23517:1, Algeria, Ideles/Hoggar; NMW 23517:2, Algeria, Ideles/Hoggar; NMW 25481, Algeria, Tit near Tamanrasset; ZFMK 20042, Algeria, Hoggar/between In Eker and In Amguel; ZFMK 20043, Niger, 20 km S Arlit/Air; ZFMK 36627, Niger, 30-40 km N Gougaran; ZFMK 36628, Niger, 30-40km N Gougaran; ZFMK 40628, Niger, near Gougaran; ZFMK 9226, Paratype of *Uromastyx geyri*, Algeria, upper Tahihaout; ZFMK 9227, Paratype of *Uromastyx geyri*, Algeria, Oued Ouhat; ZFMK 9229, Algeria, Tharemert-n-akh; ZFMK 9230, Neotype of *Uromastyx geyri*, Algeria, Gara Dienoum; ZFMK 9231, Algeria, Ahaggar/Gara Djenoum; ZMH-R04523, Algeria, Oasis Abalessa E of Tamanrasset; ZSM 4451, Paratype of *Uromastyx geyri*, Algeria, Tharemert-n-akh.

Uromastyx macfadyeni Parker, 1932

BMNH 1946.8.14.52, Paratype of *Uromastyx macfadyeni*, Somalia, Dagah Shabell 24mls SE Berbera; BMNH 1946.8.14.54, Holotype of *Uromastyx macfadyeni*, Somalia, near Berbera; BMNH 1956.1.6.55, Somalia, Heis 20 mls W Mait.

Uromastyx nigriventris Rothschild & Hartert, 1912

BMNH 1911.12.5.1, Paratype of *Uromastyx acanthinurus nigriventris*, Algeria, Ghardaia; BMNH 1911.12.5.2, Paratype of *Uromastyx acanthinurus nigriventris*, Algeria, Ghardaia; BMNH 1969.2073, Algeria, Laghouat; BMNH 1969.2074, Holotype of *Uromastyx acanthinurus nigriventris*, Algeria, Tilghempt between Laghouat and Ghardaia; BMNH 1969.2075; Algeria, Laghouat; BMNH 1969.2080, Algeria, Ain Sefra; BMNH 1969.2085, Algeria, Laghouat; BMNH 1969.2086, Algeria, Ghardaia; BMNH 1969.2087, Algeria, Laghouat; BMNH 1969.2099, Algeria, Oued N'ca; BMNH 1969.2100, Algeria, Oued N'ca; BMNH 1969.2103, Algeria, (Oued N'ca)/Oued Mya; BMNH 1969.2109, Algeria, El Hadadra between El Golea and Ghardaia; BMNH 1970. 223, Morocco, Foum el Hassane; BMNH 1970. 224, Morocco, Foum el Hassane; BMNH 1970.220, Morocco, 3 km N Tuizgui-Remz, Tarfaya; BMNH 1970.221, Morocco, 5 km E Bou Izakarn; BMNH 1972.2280, Morocco, 3 km NNW Quarzazate; BMNH 1972.2281, Morocco, 3km NNW Quarzazate; BMNH 1972.2282, Morocco, 3km NNW Quarzazate; BMNH 1972.2283, Morocco, 2 km N Douar Zednagain, 3km NNW Quarzazate; BMNH 1972.2284, Morocco, 2 km N Douar Zednagain, 3 km NNW Quarzazate; MZUF 21003, Algeria, Ghardaia; MZUF 21004, Algeria, Ghardaia; MZUF 21005, Algeria, Ghardaia; MZUF 21006, Algeria, Ghardaia; MZUF 21007, Algeria, Ghardaia; MZUF 21008, Algeria, Ghardaia; MZUF 21009, Algeria, Ghardaia; MZUF 21010, Algeria, Ghardaia; MZUF 21011, Algeria, Ghardaia; MZUF 21012, Algeria, Ghardaia; HLMD RA 1177, Morocco, SW Tizgui el Haratuine; HLMD RA 1178, Morocco, 2 km N Rich; MHNP 1927.0094, Morocco, Colomb-Bechar; MHNP 1950.204, Algeria, Beni Ounif; MHNP 1953.18, Algeria, Zerhaura Indigene Beni Abbes; MHNP 1961.249, Morocco, Assa-Aouinet Torkos; MHNP 1961.250, Morocco, vicinity Doirat; MHNP 1961.251, Morocco, Foum el Hassane; MHNP 1961.252, Morocco, Foum el Hassane; MHNP 1961.253, Morocco, 10 km S Guercif; MHNP 1961.255, Morocco, Guercif; MHNP 1961.256, Morocco, N Aouinet Torkos; MHNP 1961.257, Morocco, N Aouinet Torkos; MHNP 1961.258; Morocco, Aoinet Torkos; MHNP 1961.259, Morocco, Zagora – Tagounite; MHNP 1961.260, Morocco, Zagora – Tagounite; MHNP 1986.2013, Morocco, Bechar; MHNP 1986.2014, Morocco, Bechar; MHNP 1991.405, Morocco, Quarzazate; MHNP 1993.800, Morocco; MHNP 1994.1199, Algeria, Beni Ounif; MHNP 1994.1205, Algeria, Beni Ounif; MHNP 1994.1207, Algeria, Beni Ounif; MHNP 1994.1208, Algeria, Beni Ounif; MHNP 1994.1209, Algeria, Beni Ounif; MTKD 18981, Algeria, Ain Sefra; MTKD 20205, Morocco; Quarzazate; MTKD 27995, Algeria, Ain Sefra; NMW 14895, Algeria, Ain Sefra; NMW 14896:1, Algeria, Ain Sefra; NMW 14896:10, Algeria, Ain Sefra; NMW 14896:2, Algeria, Ain Sefra; NMW 14896:3, Algeria, Ain Sefra; NMW 14896:4, Algeria, Ain Sefra; NMW 14896:5, Algeria, Ain Sefra; NMW 14896:6, Algeria, Ain Sefra; NMW 14896:7, Algeria, Ain Sefra; NMW 14896:8, Algeria, Ain Sefra; NMW 14896:9, Algeria, Ain Sefra; NMW 21189:1, Algeria, Gardaia; NMW 21190:1, Morocco, Mazagan; NMW 21190:2, Morocco, Mazagan; NMW 21190:3, Morocco, Gus; NMW 21192:4, Algeria, Beni Abbes; NMW 21192:5, Algeria, Beni Abbes; NMW 21195:2, Algeria, Beni Mzab; NMW 21199:1, Morocco, Colomb-Bechar; NMW 21199:2, Morocco, Colomb-Bechar; NMW 21200, Morocco, Aouinet-Torkoz; NMW 21204:2, Algeria, Beni Ounif/Figuig; NMW 21205, Morocco, Colomb-Bechar; NMW 21209:1, Algeria, Beni Abbes; NMW 21209:2, Algeria, Beni Abbes; NMW 34024, Morocco, Erfoud; SMF 58031, Morocco, Oued Moulonya/36 km E Guercif; SMF 69077, Morocco, Bou Afra near Figuig; SMNS 593:1, Algeria, Ain Sefra; SMNS 598, Algeria, Oued N'za; SMNS 599, Algeria, Beni Ounif/Ouuf; SMNS 601:1, Algeria, Ain Sefra; ZFMK 18021, Algeria, S Ghardaia, Oued Sebseb; ZFMK 18022, Algeria, S Ghardaia, Oued Sebseb; ZFMK 2715, Algeria, Oued Mzab; ZFMK 2716, Algeria, Oued N'ca; ZFMK 2717, Algeria, Oued N'ca; ZFMK 2718, Algeria, Oued N'ca; ZFMK 2719, Algeria, Oued N'ca; ZFMK 2723, Morocco, Erfoud; ZFMK 2724, Morocco, Oujda; ZFMK 2725, Morocco, Oujda; ZFMK 2726, Morocco, Oujda; ZFMK 2727, Morocco, Oujda; ZFMK 2728, Morocco, Oujda; ZFMK 2729, Morocco, Oujda; ZFMK 30806, Morocco, 10 km W Tinerhir; ZFMK 41168, Algeria, Ain Sefra; ZFMK 41512, Morocco, Goulmima; ZFMK 45946, Morocco, Quarzazate; ZFMK 49661, Algeria, El Homr; ZFMK 49742, Morocco, 10-15 km NW Quarzazate; ZFMK 51077, Algeria, Ain Sefra; ZFMK 51078, Algeria, Ain Sefra; ZFMK 52356, Morocco, south of Quarzazate, Ait-Saon; ZFMK 59062, Morocco, Quarzazate; ZFMK 59063, Morocco, Quarzazate; ZFMK 59064, Morocco, Quarzazate; ZFMK 60598, Morocco, 89 km E Guelmim; ZFMK 60600, Morocco, 52 km S Guelmim; ZFMK 60602, Morocco, Erfoud; ZFMK 60603, Morocco, Erfoud; ZFMK 60605, Morocco, Erfoud; ZFMK 60606, Morocco, Erfoud; ZFMK 60607, Morocco, Erfoud; ZFMK 60608, Morocco; ZFMK 60609, Morocco, Erfoud; ZFMK 60610, Morocco, Erfoud; ZFMK 7459, Morocco, Tinerhir; ZFMK 7462, Morocco, Tinerhir; ZMH R 04527, Morocco, Erfoud; ZMH R04517, Morocco, Rissani near Erfoud; ZSM 186/1983, Algeria, Ain el Hadjadi 24 km south of Ain Sefra; ZSM 31/1981, Morocco, Tinerhir; ZSM 34/1981, Algeria, Ain Sefra; ZSM 44/1960, Morocco, Zagora; ZSM 58/1978 (1), Morocco, 25 km N Zagora; ZSM 58/1978 (2), Morocco, 25km N Zagora; ZSM 689/1979, Morocco, Ksar es Souk west of Boudenib; ZSM 8/1994, Morocco, Meski.

Uromastyx ornata

Uromastyx ornata ornata Heyden, 1827

BMNH 97.10.28.199, Egypt, Tor/ Sinai; MHNP 1909.176, Egypt, Mt. Sinai; MHNP 1909.177, Egypt, Mt. Sinai; MHNP 6954, Egypt; MHNP 6970, Egypt; NMW 21217, Egypt, Dahab; NMW 21219:1, Egypt, Sherm Scheikh; NMW 21219:2, Egypt, Sherm Scheikh; NMW 21219:3, Egypt, Sherm Scheikh; NMW 21219:4, Egypt, Sherm Scheikh; NMW 21220, Egypt, Tor; ZFMK 65174, Egypt, Wadi Feiran; ZFMK 65175, Egypt, Wadi Feiran; ZFMK 65607, Egypt; ZFMK 65609, Egypt, ZFMK 8576, Israel, Elath; ZMH R 04525, Egypt, Sinai; ZMH R 04526, Egypt, Sinai; SMF 10403, Holotype of *Uromastyx ornata*, Saudi Arabia, Mohila (Al Muwaylih).

Uromastyx ornata philbyi Parker, 1938

BMNH 1946.8.11.60, Holotype of Uromastyx philbyi, Saudi Arabia, between Mecca and Shabwa; BMNH 1946.8.11.62, Paratype of *Uromastyx philbyi*, Saudi Arabia, between Mecca and Shabwa; BMNH 1946.8.11.63, Paratype of *Uromastyx philbyi*, Saudi Arabia, between Mecca and Shabwa; BMNH 1946.8.11.64. Paratype of *Uromastyx philbyi*, between Mecca and Shabwa; BMNH 1946.8.11.65, Paratype of *Uromastyx philbyi*, Saudi Arabia, between Mecca and Shabwa; BMNH 1946.8.11.66, Paratype of *Uromastyx philbyi*, Saudi Arabia, between Mecca and Shabwa; BMNH 1964.296, Saudi Arabia, Burayman 21°40'N 39°10'E; BMNH 1975.518, Saudi Arabia, Bazzah 22°00'N 39°30'E; BMNH 1975.519, Saudi Arabia, Burayman 21°39'N 39°13'E; BMNH 1976.1748, Saudi Arabia, Wadi Fatma; BMNH 1979.960, Saudi Arabia, Burayman 21°45'N 39°15'E; BMNH 1985.882, Saudi Arabia, Mecca by pass km 91 / 21°14'N 29°48'E; BMNH 1985.884, Saudi Arabia, Mecca by pass km115 / 21°15,5'N 39°55'E; BMNH 1986.434, Saudi Arabia, 21°14'N 39°55'E; BMNH 1986.436, Saudi Arabia, 16 km N of Jeddah; BMNH 1975.518, Saudi Arabia, Bazzah 22°N 39°30'E; BMNH 1980.55, Saudi Arabia, Jabal as Sinfa; MZUF 27884, Yemen, Ju Amlah 26 km NW Sa'dah; MZUF 27885, Yemen, Ju Amlah 26 km NW Sa'dah; MZUF 27906, Yemen, Ju Amlah 26 km NW Sa'dah; MZUF 28187, Yemen, Ju Amlah 26 km NW Sa'dah; MHNG 2457.33, Saudi Arabia, Jebel Hababa; MHNG 2457.34, Saudi Arabia, Jebel Hababa; MHNG 2457.35, Saudi Arabia, Wadi Sawawin; MHNG 2536.49, Saudi Arabia, Makkah by pass km 56; MHNP 4318, Saudi Arabia, Jeddah; ZFMK 84442, Saudi Arabia, 19°05'N 41°50'E.

Uromastyx ocellata Lichtenstein, 1823

BMNH 1914.5.14.13, Sudan, Sinkat; BMNH 1927.8.13.38, Sudan, Merowe/Dongola; BMNH 1927.8.13.39, Sudan, Merowe/Dongola; BMNH 1937.12.5.117, Somalia, Borama District; BMNH 1937.12.5.118, Somalia, Borama District; BMNH 1937.12.5.119, Somalia, Borama District; BMNH 1937.12.5.121, Somalia, Borama District; BMNH 1937.12.5.122, Somalia, Borama District 42°45'N 10°45'E; BMNH 1937.12.5.123, Somalia, Borama District 42°45'N 10°45'E; BMNH 1937.12.5.124, Somalia, Borama District 42°55'E 10°55'N; BMNH 1937.12.5.125, Somalia, Borama District 42°55'E 10°55'N; BMNH 1937.12.5.127, Somalia, Borama District 43°E 11°N; BMNH 1937.12.5.128, Somalia, Borama District 43°E 11°N; BMNH 1937.12.5.130, Somalia, Borama District; BMNH 1953.17.63, Sudan, Tehamiyam; BMNH 1953.17.64, Sudan, Tehamiyam; BMNH 1953.17.65, Sudan, Tehamiyam; BMNH 97.10.28.202, Sudan, Suakim; BMNH 97.10.28.203, Sudan, Suakim; BMNH 97.10.28.204, Sudan, Suakim; BMNH 97.10.28.205, Sudan, Suakim; BMNH 97.10.28.206, Sudan, Suakim; BMNH 97.10.28.207, Sudan, Suakim; BMNH 97.10.28.208, Sudan, Suakim; BMNH 97.10.28.209, Sudan, Suakim; MHNP 1897.348, Egypt; MHNP 1897.349, Egypt; NMW 21215, Oasis Harar; NMW 21216, Sudan, Suakim; ZFMK 20822, Sudan, Suakin; ZFMK 38396, Sudan, 40 km W Suakim direction Sinkat; ZMB 811, Holotype of *Uromastyx ocellata*, Sudan, Nubia; ZSM 219/1976, Sudan, Dongola Province.

Uromastyx princeps O'Shaughnessy 1880

BMNH 1931.7.20.270, Somalia, 11°5'N 49°0'E; BMNH 1931.7.20.272, Somalia, 8°54'N 48°54'E; BMNH 1931.7.20.273, Somalia, Buran District 10°13'N 48°46'E; BMNH 1931.7.20.274, Somalia, 10°22'N 49°0'E; BMNH 1931.7.20.275, Somalia, 10°42'N 49°E; BMNH 1946.814.56, Holotype of *Uromastyx princeps*, Zanzibar (unreliable Locality, Wilms 2001); BMNH 1956.1.3.9, Somalia, Wachderria 45mls E Mait; BMNH 1961.1655, Somalia, Candala/Migiurtina; BMNH 1961.1656, Somalia, Candala/Migiurtina; BMNH 1983.735, Somalia, 5°56'N 48°55'E; MZUF 23691, Somalia, Scusciuban; MZUF 10536, Somalia, District of Alula; MZUF 23673, Somalia, Bur Dagner; MZUF 23674, Somalia, Bur Dagner; MZUF 23675, Somalia, Meleden; MZUF 23676, Somalia, Sukorre; MZUF 23686, Somalia, Carin-Gié Bahaia; MZUF 23690, Somalia, Scusciuban; MZUF 23692, Somalia, Monti Carcar; MZUF 23693, Somalia, Scusciuban; MZUF 23694, Somalia, Scusciuban; MZUF 23695, Somalia, Scusciuban; MZUF 23696, Somalia, Scusciuban; MZUF 23782, Somalia, Passo del Didim S of Carin; MZUF 5497, Somalia, Valle di Run; MZUF 5623, Somalia, Valle di Run; MZUF 739, Somalia, Passo del Didim S of Carin; MHNP 1966.1071, Somalia, Candala; MHNP 1966.1072, Somalia, Candala; MHNP 5732, Yemen, Aden (unreliable Locality); MHNP 5831, Somalia, Bender Meraya; MHNP 5832, Somalia, Bender Meraya ; SMF 22931, Somalia, Benden Cassim Migiurtinia; ZFMK 58048, Somalia, Bossasa; ZFMK 58985, Somalia, Bossasa.

Uromastyx shobraki Wilms & Schmitz, 2007

BMNH 1938.2.1.47, Country not reliably traceable, southern Hejaz; BMNH 1987.854, Yemen, Tihama Taiz; BMNH 1988.54, Yemen, Mafraq-Al Mokka km 13,5; BMNH 1988.55, Yemen, Mafraq-Al Mokka km 13,6; MZUF 33614, Yemen, Mafraq-Al Mokka km 13,6; MZUF 33615, Yemen, Mafraq-Al Mokka km 13,5; MHNG 2455.100, Paratype of *Uromastyx yemenensis shobraki*, Yemen, Mafraq-Al Mukha 13,5km; MHNG 2464.44, Yemen, Mafraq-Al Mokka km 13,5; MHNG 2496.55, Paratype of *Uromastyx yemenensis shobraki*, Yemen, between Mocca and Wadi Zabid; MHNG 2496.56, Paratype of *Uromastyx yemenensis shobraki*, Yemen, between Mocca and Wadi Zabid; MHNG 2527.92, Yemen, Wadi Zabid; MHNG 2538.47, Yemen, Wadi Zabid; MHNG 2542.13, Yemen, Wadi Zabid; MHNG 2542.14, Yemen, Wadi Zabid; MHNG 2553.56, Paratype of *Uromastyx yemenensis shobraki*, Yemen, Mafraq-Al Mokka km 1,5, MTKD 31624, Yemen, North Yemen; MTKD 32847, Yemen, North Yemen; ZFMK 48680, Paratype of *Uromastyx yemenensis shobraki*, Yemen, Mafraq-Al Mokka km 13,6; ZFMK 48681, Holotype of *Uromastyx yemenensis shobraki*, Yemen, Mafraq-Al Mokka km 13,5; ZFMK 55651, Yemen, North Yemen; ZFMK 55652, Yemen, North Yemen; ZFMK 58047, Yemen, North Yemen; ZFMK 60687,Yemen, North Yemen; ZFMK 73676, Yemen, Mafraq - al Mocca; ZFMK 73677, Yemen, Mafraq - al Mocca.

Uromastyx thomasi **Parker, 1930**

BMNH 1931.7.16.46, Oman, Wadi Hauf; BMNH 1946.8.14.43, Holotype of *Uromastyx thomasi*, Oman, BU'Juay; BMNH 1954.1.2.98, Oman, Ras Duggum; BMNH 1956.1.16.8, Bahrein (unreliable locality); BMNH 1971.1354, Oman, W of Bai; BMNH 1971.1355, Oman, W of Bai; BMNH 1973.2908, Oman, Masirah; BMNH 1975.1038, Oman, Masirah; BMNH 1977.335, Oman, Jiddat al Harasis 19°32'N 57°12'E; BMNH 1978.1322, Oman, Al Ajaiz; BMNH 1978.2249, Oman, near Haql 20°25'N 58°47'E; BMNH 1980.213, Oman, Thamarit 17°38'N 54°02'E; BMNH 1980.570, Oman, Jiddat al Harasis 19°32'N 57°13'E; BMNH 1982.1221, Oman, Masirah.

Uromastyx yemenensis **Wilms & Schmitz, 2007**

BMNH 1946.8.11.68, Paralectotype *Uromastyx benti*, Yemen, Makulla Hadramaut (doubtful record); BMNH 1963.755, Yemen, Wadi Tiban west of Aden; BMNH 95.11.27.6, Yemen, Hills 50 km from Aden; BMNH 95.11.27.7, Yemen, Hills 50 km from Aden; BMNH 99.12.13.106, Yemen, between Mount Manif and Jimil / N. of Lahej; BMNH 99.12.13.51,Yemen, Yabian mountains, MTKD 24554, Yemen, Zingibar, Abyan-Gouvernement; MTKD 25441, Yemen, Amran/Aden; MTKD 26951, Yemen, Lawdar, Abyan-Gouvernement, MTKD 26952, Yemen, Lawdar, Abyan-Gouvernement; MTKD 28873, Yemen, Lawdar, Abyan-Gouvernement; MTKD 29475, Paratype of *Uromastyx yemenensis*, Yemen, Zingibar, Abyan-Gouvernement; MTKD 34675, Yemen, Abyan-Gouvernement; ZFMK 47860, Paratype of *Uromastyx yemenensis*, Yemen, Lawdar, Abyan-Gouvernement; ZFMK 47861, Holotype of *Uromastyx yemenensis*, Yemen, Lawdar, Abyan-Gouvernement; ZFMK 49036, Paratype of *Uromastyx yemenensis*, Yemen, Lawdar, Abyan-Gouvernement.

APPENDIX III.

Morphological character coding

(A) Number of tail worls

(0) = 29–36 Whorls

(1) = 15–28 Whorls

(2) = 9–13 Whorls

The taxon *hardwickii* has 29–36 primary tail whorls. In *Leiolepis* more than 100 scale rows are always present from the cloacal slit to the tip of the tail. Therefore the character state present in *hardwickii* is considered to be plesiomorphic (0).The majority of the taxa (with the exception of *princeps* and *thomasi*) have 15–28 primary tail whorls (1). The short tailed taxa *princeps* amd *thomasi* are considered to show a character state derived from state 1 (2).

(B) Number of gular scales

(0) = > 29.7

(1) = < 25.9

With the exception of *ornata* and *philbyi*, all taxa have an average count of more than 29.7 gular scales. In *Leiolepis* between 33–45 gular scales are present. Therefore high numbers of gular scales are considered to be the plesiomorphic character state (0). In *ornata* and *philbyi* average gulare scale counts are 25.9 and 22.6 respectively (1).

(C) Number of scales around midbody

(0) = 140–220

(1) = 265–319

With the exception of *aegyptia*, *microlepis*, *leptieni* and *occidentalis* all taxa have an average scale count of less than 220 scales around midbody. *Leiolepis* has between 165–211 scales around midbody. Low scale counts are therefore considered to be the plesiomorphic character state (0). The high scale counts present in the taxa of the *U. aegyptia* group are considered to be apomorphic (1).

(D) Number of ventral scales between gular and inguinal fold

(0) = < 121

(1) = > 121

With the exception of *aegyptia*, *microlepis*, *leptieni* and *hardwickii* all taxa have an average number of ventral scales of less than 121. *Leiolepis* either has less than 100 ventral scales. Low numbers of ventral scales are therefore considered to be the plesiomorphic character state (0), while high numbers of ventral scales are considered to by apomorphic (1).

(E) Number of scales around 5th tail whorl

(0) = 46.2

(1) = < 37

In average *hardwickii* has 46.2 scales around the 5th tail whorl (Range: 40–52). Average values of all remaining taxa are considerably lower (between an average of 22.8 and 36.7). In *Leiolepis* the respective value is 71–125 scales. A high number of scales is therefore considered to be the plesiomorphic character state (0). All remaining taxa have low numbers of scales and are therefore considered to show the apomorphc character state (1). Only in three taxa (*microlepis, yemenensis* and *shobraki*) single specimens might show values overlapping with the range of *hardwickii* (43 scales for *microlepis*, 40 scales for *shobraki* and *yemenensis*).

(F) Number of scales between subocularia and supralabialia

(0) = > 3.6

(1) = < 3.2

Most taxa have 3–9 scales between the subocularia and supralabialia. In *Leiolepis* 5–7 scales are present. A high scale count is therefore considered to be the plesiomorphic character state (0). Only two taxa (*princeps* and *thomasi*) show scale counts as low as two scales. In both taxa average scale counts are lower than in the remaining taxa (*princeps* 3.2 / *thomasi* 3.0). This character state is considered to be apomorphic (1). From the remaining taxa only *geyri* and *ornata* have less than four scales between subocularia and supralabialia (*ornata*: 3.7; *geyri*: 3.6).

(G) Snout-vent-length (SVL)

(0) = < 28.0 cm

(1) = > 35.5 cm

Species of the genus *Leiolepis* can reach the following maximum snouth-vent-length: *belliana*: 16.6 cm; *reevesii*: 15.1cm; *peguensis*: 13.6 cm; *triploida*: 14.8 cm and *guttata*: 18.4 cm (Peters 1971). Taxa of the genus *Uromastyx* reach a maximum SVL of: *acanthinura*: 25.3 cm; *nigriventris*: 24.0 cm; bei *aegyptia*: 40.0 cm; *asmussi*: 26.5 cm; *alfredschmidti*: 23.0 cm; *benti*: 19.6 cm; *yemenensis*: 18.5 cm; *shobraki*: 20.8 cm; *dispar*: 23.1 cm; *flavifasciata*: 28.0 cm; *maliensis*: 23.2 cm; *microlepis*: 35.5 cm; *macfadyeni*: 11.7 cm; *geyri*: 19.3 cm; *hardwickii*: 23.3 cm; *loricata*: 27.7 cm; *leptieni*: 37,5 cm (Wilms & Böhme 2007); *ocellata*: 17.4 cm, *ornata:* 19.6 cm; *philbyi*: 19.2 cm; *princeps*: 15.4 cm and *thomasi*: 18.2 cm. A maximum SVL of less than 28 cm is considered to be the plesiomorphic character state (0), while a maximum SVL of 35.5 cm or more is considered to be the apomorphic character state (1). Because of the very limited knowledge on the maximum length of *Uromastyx occidentalis* and the supposed relationship of this species with the large growing taxa of *Uromastyx aegyptia* we assign apomorphic character state to this taxon.

(H) Tail length

(0) = > 52.6 % of SVL

(1) = < 42.9 % of SVL

The character „short tailed“ in *princeps* and *thomasi* is considered to be apomorphic (1) because this character state is exceptional within the genus *Uromastyx* and all species of the outgroup possess long tails (0).

(I) Tail scalation

(0) = last 2–8 whorls consisting of continuous scale rows

(1) = last 12–21 whorls consisting of continuous scale rows

The members of the *Uromastyx ocellata* group (*ocellata*, *ornata*, *philbyi*, *benti*, *yemenensis*, *shobraki*) as well as *macfadyeni* show a very unique scalation of the tail, with the last 12–21 whorls consisting of continuous scale rows in which one dorsal scale row corresponds with one row ventrally (1). In all other taxa the character „continous scale row on the tail“ is restricted only to the last 2–8 whorls. All other whorls in these taxa consist of one dorsal scale row with more than one corresponding scale rows ventrally. The latter character state is considered to be plesiomorphic (0), because it can easily be derived from the tail of a *Leiolepis* with its scalation consisting of small scales.

(J) Value of the quotient of head width and head length

(0) = 0.861–0.875

(1) = 0.897–0.952

(2) = 0.967–0.997

Within the genus *Leiolepis* this quotient values between 0.66–0.75. A low average value is considered to be a plesiomorphy. Therefore *princeps* (value: 0.875), *thomasi* (value: 0.874) and *yemenensis* (value: 0.861) possess the plesiomorphic character state (0), but which is not assigned to *yemenensis* for the phylogenetic analysis because of the proven relationship of *yemenensis* to the *ocellata* group within *Uromastyx* [*yemenensis*: (1)]. Most of the remaining taxa (exceptions *hardwickii*, *asmussi*, *loricata*) have average values for this quotient ranging between 0.897–0.952 which are considered to be the apomorphic character state (1). The relatively broad headed taxa *asmussi*, *loricata* and *hardwickii* posses values for this quotient rangeing between 0.967–0.997. This character state is considered to be different from (1) and is therefore assigned to (2).

(K) Value of the quotient of tail length and maximun with of the tail at the 5th whorl

(0) = 4.4–5.2

(1) = 3.4–3.9

(2) = 1.2–2.1

The average value of this quotient within most taxa is between 4.4 bis 5.2. In the genus *Leiolepis* the respective values are between 15 and 20, therefore higth values are considered to be plesiomorphic (0).

For *acanthinura*, *nigriventris*, *dispar*, *flavifasciata*, *maliensis*, *macfadyeni* and *philbyi* the average value is between 3.4 and 3.9. These character states are considered to be apomorphic (1). For the two short tailed taxa *thomasi* and *princeps* the values are 1.2 and 2.1 respectively. These character states are considered to be different to (1) and are therefore assigned to (2).

(L) Enlarged tubercular scales on the dorsum

(0) = tubercular scales absent

(1) = tubercular scales present

Leiolepis lacks enlarged tubercular scales on the dorsum. Within the taxa in question only *hardwickii*, *loricata* and *asmussi* possess enlarged tubercular scales. This character state is considered to be apomorphic (1).

(M) Intercalary scales between tail whorls dorsally

(0) = intercalary scales present

(1) = intercalary scales absent

In *Leiolepis* tail scalation is not arranged in whorls. Therefore the presence of intercalary scales is considered to be the plesiomorphic character state, because their presence is easily derived from a tail witch is consisting of small scales (0). The apomorphic character state shows a reduction and enlargement of scale rows on the tail (1).

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Some New and Interesting "Microlepidoptera" from the Collection of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn (Lepidoptera: Tineidae, Epermeniidae, Acrolepiidae, Douglasiidae)

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Abstract. The study of some of the so called "Microlepidoptera" families, the Tineidae, Epermeniidae, Acrolepiidae and Douglasiidae, at the collection of the ZFMK, brought some species of taxonomical and faunistical interest to light. Two species are described as new: *Reisserita zouhari* sp. n. (Tineidae), and *Epermenia (Epermenia) dalianicola* sp. n. (Epermeniidae), and the type-material of the four families, represented in this collection, is listed and commented.

Keywords. Tineidae, Epermeniidae, Acrolepiidae, Douglasiidae, new species, type material.

The courtesy of my colleague Dr. Dieter Stüning, curator of the Lepidoptera collection at the Zoologisches Forschungs-museum Alexander Koenig, Bonn, enabled me to study the material of the four families Tineidae, Epermeniidae, Acrolepiidae and Douglasiidae, stored at this collection.

The paper includes descriptions of two new species, a list of taxa represented by type-specimens and comments on some additional species which are of faunistical interest.

TINEIDAE

Scalidomia hoenei Petersen, 1991
Holotype ♂, [China, Jiangsu]. "Lungtan b. Nanking, Prov. Kiangsu, 25. IX. 1933, H. Höne"; Paratype ♂ same location and collector, but 22. VIII. 1933.

Known from the type locality only.

Rhodobates sinensis Petersen, 1987
Holotype ♂, [China, Yunnan]. "Li-kiang, Prov. N. Yünnan, 18. VII. 1934, H. Höne".

The collection contains numerous additional specimens from the type locality and from other locations in China:

12 ♂, 28 ♀, Prov. Nord-Yuennan, Li-kiang, between 28. V. and 17. VIII. 1934, leg. H. Höne; 2 ♂, Shanghai, 10. V. 1933, leg. H. Höne; 1 ♂, Kuling, 2. V. 1934, leg. H. Höne; 1 ♀, Prov. Shantung, Laushan bei Tsingtau, 6. VI. 1936, leg. H. Höne; 1 ♂ Batang (Tibet), Tal des Yangtze, ca. 2800 m, 9. VII. 1936, leg. H. Höne.

The female genitalia were illustrated for the first time by LI & XIAO (2006). It is of interest, that the authors collected a large series of this species at the type locality, after more than 70 years.

Morophaga formosana Robinson, 1986
[= *kobella* Robinson, 1986]

1 ♂, [China, Jiangsu]. "Shanghai, Provinz Kiangsu, 30. V. 1935, H. Höne"

Distribution. First record from the Palaearctic region; previously known only from the type locality (Taiwan) and from Fu-chou (China, Fujian).

Nemapogon gliriella (Heyden, 1865)
[= *cachetiellus* Zagulajev, 1963; = *cacheticus* Zagulajev, 1964; = *ibericus* Zagulajev, 1968]

1 ♂ Düsseldorf-Eller, 6. VII. 1941, leg. Friedel. New record for Nordrhein-Westfalen.

Distribution. The species is hitherto known from Germany, Austria, Czech Republic, Slovakia, Slovenia, Turkey and the Caucasus region (Georgia, Armenia). Every time, only few specimens were collected.

Biology. Larvae feed in fungi *Stereum hirsutum* (BETTAG 1995; BETTAG & BASTIAN 1996), *Stereum rugosum* (C.Vetter, Hamburg, 1996 in litt.).

Edosa spinosa (Gaedike, 1984)
Holotype ♂, [China, Shaanxi]. "Tapaishan im Tsinling, Prov. Süd-Shensi, 1700 m, 16. VI. 1936, H. Höne".

Distribution. Known from the type locality only.

Edosa sinica (Gaedike, 1984)
Holotype ♂, [China, Jiangsu]. "Prov. Kiangsu, Lungtan bei Nanking, 23. V. 1933, H. Höne". Paratypes: 4 ♂, same location, but 20., 22., 28. V. 1933, leg. H. Höne.

Distribution. Known from the type locality only.

***Reisserita zouhari* sp. n.** (Fig. 1)
Holotype ♂, "Aegyptus Mariput El Agami, 9. 5. 1975, Ing. Vlad. Zouhar lgt.;" "Museum A. Koenig Ein[gang] Nr. 90/283 ex Coll. Zouhar;" "Gen. präp. [genitalia slide] Gaedike Nr. 5644;" "Holotypus ♂ *Reisserita zouhari* sp. n. det. R. Gaedike 2007"

Description. Wingspan 12 mm; head, palpi, thorax light ochre, basal area of tegulae darker; forewing light ochre, too, without any pattern, first half of costa darker.

Male genitalia (Fig. 4). Uncus bilobate, each lobus with pointed end, between the lobi with deep incision; gnathus arms hooke-shaped, pointed, broadest in the middle; tegumen and vinculum broad, saccus nearly triangular, apically rounded; valva with long narrow transtilla, corpus divided into two processus, one short processus at beginning of the costa, the second one longer, hook-shaped, pointed, the view depending on the preparation; aedeagus as long as the whole genitalia, narrow, with two slightly curved cornuti.

Female gentalia. Still unknown.

Remarks. The new species is similar to *Reisserita mauritanica* (Baker, 1885), but the structure of uncus (deep incision, pointed lobi), and valva, the shorter and broader gnathus arms and the aedeagus with two cornuti make it distinguishable.

The new species is named in honour of the collector, Mr. Vladimir Zouhar.

Praeacedes atomosella (Walker, 1863)
[= *seminolella* Beutenmüller, 1889; = *thecophora* Walsingham, 1908; = *despecta* Meyrick, 1919; = *deluccae* Amsel, 1955; = *malgassica* Gozmány, 1970; = *decui* Capu?e & Georgescu, 1977]

5 ♂, 2 ♀, Egypt. Kahira-Garden city; Wadi El Natrun, between 1970 and 1974, leg. V. Zouhar.

Distribution. Pantropical (ROBINSON & NIELSEN, 1993). Palaearctic region including the Canary Islands; Azores; Malta; Cyprus; Egypt.

Biology. The larvae feed from characteristic flattened, elongate oval cases composed of fibers and detritus and lined with silk. They are similar to those of *Phaereoeca allutella* (Rebel) but in average smaller and more rounded at proximal end. The cases can be found at house walls. The feeding habit is not known with certainty, but probably the larvae are chitinophagous like those of *P. allutella* (ROBINSON & NIELSEN 1993; O. Karsholt, Copenhagen, pers. observ. 2000). A detailed description of the larva is given by HINTON & BRADLEY (1956) under the name *Titaenoses thecophora*.

Tinea subalbidella Stainton, 1867
[= *arcanella* Zagulajev, 1960; = *liberiella* Zeller, 1879; = *excavata* Meyrick, 1914; = *frugivora* Meyrick, 1917; = *insectivora* Meyrick, 1932]

1 ♂, Egypt. Kahira-Garden city, 25. IX. 1974, leg. V. Zouhar.

New record for Egypt.

Distribution & biology. According to ROBINSON (1989), who in detail described the distribution and the biology, the species is known from Palaearctic (Pakistan), Oriental (Thailand, India, Sri Lanka) and Afrotropical (Sierra Leone, Nigeria) regions. Specimens were reared from monkey skins, the pelt of a wild cat, horns and dead Orthoptera. In Thailand, larvae shared nests with an infestation of *Monopis longella*. They behaved in a similar way to those of *M. longella*, tunnelling in the feathers and pupating just below the nest surface in a cylindrical cocoon of thin silk with adhering fragments of feathers.

Tinea omichlopis Meyrick, 1928
[= *nonimella* Zagulajev, 1955]

2 ♂, [China, Shaanxi]. "Tapaishan im Tsinling, Süd-Shensi, 28., 31. V. 1935, H. Höne".

Distribution. Hitherto known throughout the Palaearctic region from Italy, Balkan peninsula, Central Europe to Caucasus region, Middle to Far East. First record for China.

Niditinea sinensis Petersen & Gaedike, 1993
Holotype ♂, [China, Jiangsu]. "Prov. Kiangsu: Shanghai, 19. IX. 1943, H. Höne".

Paratypes. 3 ♂, same location, but 19. VIII., 9., 17. IX. 1942, leg. H. Höne.

Distribution. Known from the type locality only.

Crypsithyris japonica Petersen & Gaedike, 1993
Holotype ♂, Japan, Unzen, 15. VII. 1937, leg. H. Höne.

Distribution. Known from the type locality only.

Crypsithyris hoenei Petersen & Gaedike, 1993
Holotype ♂, [China, Yunnan]. „Li-kiang, Prov. Nord-Yuennan, 22. VI. 1934, H. Höne". Paratype: 1 ♂, same location, but 4. VII. 1934, leg. H. Höne. One additional ♂ from the type location.

Distribution. Known from the type locality only.

Monopis megalodelta Meyrick, 1908 (Fig. 2)
1 ♂, Türkei, Bedirge, 4. V. 1968, leg. Mittendorf.

Distribution. Previously known only from the Afrotropical region, first record from the Palaearctics.

The species is superficially similar to *M. monachella* (Hübner, 1796), but the shape of the white area on forewing is distinctly different, other differences are seen in the structure of the genitalia (Fig. 5).

Monopis trapezoides Petersen & Gaedike, 1993
Holotype ♂, [China, Zhejiang]. „Prov. Chekiang, West Tien-mu-shan, 15. IX. 1932, H. Höne". Paratypes: 2 ♂, same location and collector, but 3., 5. IX. 1932.

Distribution. Known from the type locality only.

Gerontha hoenei Petersen, 1987
Holotype ♂, [China, Yunnan]. „Li-kiang, Prov. N-Yuennan, 31. VII. 1935, H. Höne". Paratypes: 2 ♂, same locality, but 26. VII., 2. VIII. 1935, leg. H. Höne; 1 ♂ China, West Tien-mu-shan, Prov. Chekiang, 2. VIII. 1932, leg. H. Höne. Additionally 3 specimens from the type locality.

Distribution. Known from the type locality only.

Tinissa insularia Robinson, 1976
Paratypes. 1 ♂, 1 ♀, NO-Sumatra, Dolok Merangier, 180 m, September 1969, 9.I.–2.II.1970, leg. Diehl; 1♀ N-Sumatra, Ketambe, 40 km NW of Kutatjane, 300–500 m, 10.–18.VI.1972, leg. Roesler & Küppers.

Distribution. Known from the type localities: Java, Malaya, Borneo, Celebes, Moluccas, Philippines, New Guinea, Solomon Islands, Sumatra.

EPERMENIIDAE

Epermenia (Epermenia) dalianicola sp. n. (Fig. 3)
Holotype ♂, "China. Luda, Dalian, 10. 5. 1959, Ing. VLAD. ZOUHAR lgt.;" "Museum A. Koenig Eing.[ang] Nr. 90/283 ex Coll. Zouhar;" "Gen. präp. [genitalia slide] Gaedike Nr. 5832;" "Holotypus ♂ *Epermenia (Epermenia) dalianicola* sp. n. det. R. Gaedike 2008;"

Paratype. Without abdomen, same location, but 29. 4. 1959, "Museum A. Koenig Eing.[ang] Nr. 90/283 ex Coll. Zouhar;""Paratypus *Epermenia (Epermenia) dalianicola* sp. n. det. R. Gaedike 2008;"

Description. Wingspan 11 mm; head, palpi, thorax dark grey, tips of the scales whitish; scales on forewing whitish at base, distal half dark grey; on dorsum at 1/3 and 1/2 a tuft of raised black scales; fringe with two black lines in the middle and apically; on the cell, before and behind 1/2 and at 3/4, three light brown dots present, the apical dot is the largest; obliquely above the two tufts, indications of additional very small brown dots are present; hindwing light grey.

The holotype is somewhat lighter, because the pattern is rubbed.

Male genitalia (Fig. 6). Uncus long, narrow, slightly curved, with pointed tip; tegumen broad, apical edge and the middle stronger sclerotized than the other part; valva with small transtilla, ampulla broad, curved, with a blunt tip, basally with a strong sclerotized edge; cucullus broad, rounded; sacculus apically with a very small pointed tip below the sclerotized edge of ampulla; aedeagus shorter than valva, with a hooked cornutus.

Female genitalia. Still unknown.

Remarks. The new species is superficially similar to *E. ochreomaculella asiatica* Gaedike, 1979, but clearly distinguishable by the structure of the genitalia, especially the shape of the ampulla.

The species is named after the location of the types: Dalian.

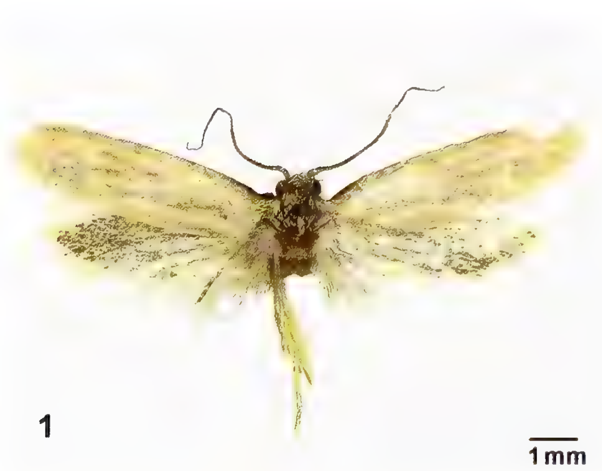
Epermenia (Cataplectica) sinica Gaedike, 1996
Holotype ♂, [China, Yunnan]. „Li-Kiang, Prov. Nord-Yuennan, 19. VII. 1934, H. Höne".

Distribution. Known from the type locality only.

Ochromolopis kaszabi Gaedike, 1973
1 ♂, [China, Hunan]. "Prov. Hunan, Hoengshan, 15. IV. 1933, H. Höne".

New record for China.

Distribution. Hitherto known from eastern parts of the Palaearctic region (Mongolia, Siberia, Russian Far East).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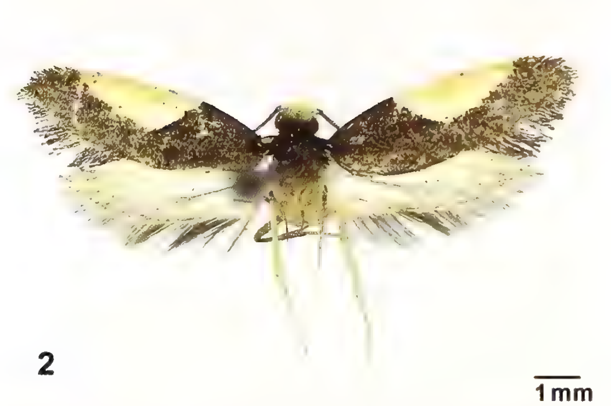
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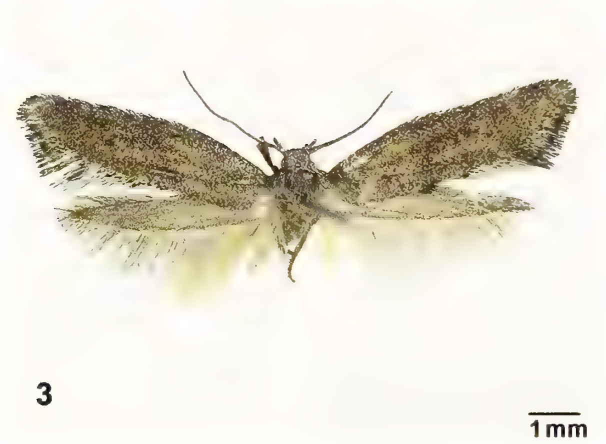
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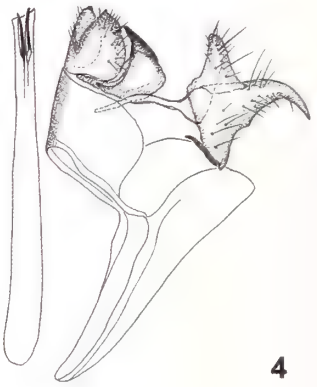
Figs 1–3. **1.** *Reisserita zouhari* sp. n.; **2.** *Monopis megalodelta* Meyrick, 1908; **3.** *Epermenia (Epermenia) dalianicola* sp. n.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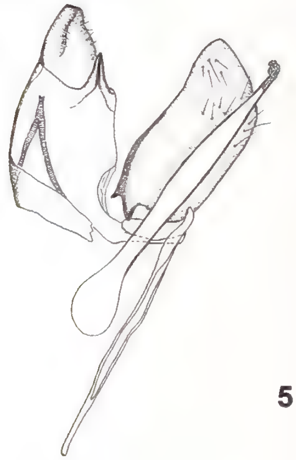
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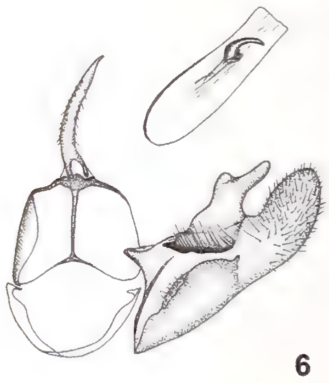
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Figs 4–6. **4.** *Reisserita zouhari* sp. n., male genitalia (aedeagus separated); **5.** *Monopis megalodelta* Meyrick, 1908, male genitalia (left valva removed); **6.** *Epermenia (Epermenia) dalianicola* sp. n., male genitalia (left valva removed, aedeagus separated).

ACROLEPIIDAE

Digitivalva (Digitivalva) asiatica Gaedike, 1971
Holotype ♂, [China, Shaanxi]. "Tapaishan im Tsinling, Süd-Shensi, 1. VII. 1935, H. Höne";

3 ♂, China, Li-kiang, Prov. Nord-Yuennan, 18. VI., 10. VII., 13. VIII. 1934, leg. H. Höne

First record besides the holotype.

Distribution. China: Shaanxi, Yunnan.

Digitivalva (Digitivalva) hoenei Gaedike, 1971
Holotype ♂, [China, Yunnan]. „Li-kiang, Prov. Nord-Yuennan, 10. VIII. 1934, H. Höne". Paratype: 1 ♀, same location, but 8. VII. 1934, leg. H. Höne; one additional specimen from the type locality.

Distribution. Known from the type locality only.

Acrolepiopsis sinense Gaedike, 1971
Holotype ♂, [China, Zhejiang]. „Wenchow (Chekiang), 12. IV. 1934, H. Höne".

Paratype. 1 ♀, same data.

Distribution. Known from the type locality only.

Acrolepiopsis deltoides Gaedike, 1971
Holotype ♂, [China, Zhejiang]. „West Tien-mu-shan, Provinz Chekiang, 4. IX. 1932, H. Höne.

Distribution. Known from the type locality only.

DOUGLASIIDAE

Tinagma anchusellum (Benander, 1936)
1 ♂, Jordanien, Amman, 25. III. 1968, leg. S. u. J. Klapperich; 1 ♀, O-Jordanien, Zerkatal bei Romana, 15. III. 1966, leg. S. u. J. Klapperich: New record for the country.

Distribution. Known from North Europe (Sweden, Denmark, Estonia, Latvia) through Central Europe and Balcan peninsula (Greece) to Cyprus, Bulgaria, Ukraine, further from Turkey and the Caucasus region (Armenia, Azerbaidshan).

Biology. Larvae are mining on *Anchusa officinalis*.

Tinagma balteolellum (Fischer von Roeslerstamm, 1841)
[= *borkhauseniella* Herrich-Schäffer, 1855]
1 ♂, Jordanien, Amman, 4. IV. 1968, leg. S. u. J. Klapperich. New record for Jordania.

Distribution. Known from nearly whole Europe, except northern part, and outside of Europe from Morocco.

Biology. Larvae are mining in stems of *Echium vulgare* and *E. biebersteini*.

Tinagma klimeschi Gaedike, 1987
32 ♂, Aegyptus, Alexandria, 25., 26. II. 1973; 2. III. 1974, leg. V. Zouhar;

1 ♂, Israel, Latroun bei Jerusalem, 25. III. 1968, leg. Bleszynski.

New record for the two countries.

Distribution. Hitherto known only from Rhodos (type-locality) and from Cyprus.

Biology. Larvae are mining on *Echium diffusum*.

Tinagma minutissimum (Staudinger,1880)
1 ♂, Volgograd, 18.–24. V. 1967, leg. V. Zouhar

Distribution. Previously known only from the type locality (Turkey: Amasia) and from Crimea.

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Islands Between the Realms: A Revised Checklist of the Herpetofauna of the Talaud Archipelago, Indonesia, with a Discussion About its Biogeographic Affinities

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Abstract. Since the last taxonomic account was published 80 years ago, we provide the first updated annotated checklist for the herpetofauna of the remote Talaud Archipelago, which lies between the biogeographic realms of Sulawesi, the Philippines, and the Moluccas. We report on a small collection from Pulau (= island) Salibabu, the second largest island within the Talaud Archipelago, which, until recently, was one of the least-known areas of the Sulawesi region. In total, 37 specimens representing three anuran species, 11 lizard species (four geckos, four skinks, two agamids, and one monitor lizard species), and two snake species were collected. Of these, six species, viz. one microhylid frog (*Callulops* cf. *dubius*), three lizard species (*Nactus* cf. *pelagicus*, *Gehyra mutilata*, and *Eutropis* cf. *rudis*), and two snake species (*Typhlops* sp. and *Boiga irregularis*), are recorded here for the first time for the Talaud Islands, while *Hydrosaurus* sp., *Cyrtodactylus* cf. *jellesmae*, *Eutropis multicarinata* and *Emoia atrocostata* have not been previously known from Salibabu Island. Novel records for Talaud are completed by *Hemidactylus frenatus* and *Eutropis multifasciata* from the MCZ online database. A historical record of *Gekko vitattus* may be incorrect but seems possible given the biogeographic distribution patterns of Australopapuan amphibian and reptile species discussed in this paper. Historical reports of *Candoia* reaching North Sulawesi appear dubious. Combined with previous records, the herpetofauna of Talaud currently comprises 27 species of amphibians and reptiles that include three different species of frogs, 17 lizards (five geckos, eight skinks, three agamids, and one varanid), five snake species as well as one sea turtle and one crocodile. Two historical records of *Gekko vittatus* and *Bronchocela jubata*, respectively, require verification.

Finally, the zoogeographic affinities of the Talaud Islands and their implications for the course of past dispersal routes between the Philippines, North Sulawesi and the northern Moluccas are discussed in the light of herpetofaunistic distribution patterns compared with those shown by other groups of organisms.

Keywords. Wallacea, Sulawesi region, amphibians, reptiles, biogeography, endemism.

Abstrak (Bahasa Indonesia). Kami memperbaharui daftar jenis-jenis herpetofauna yang ditemukan di Kepulauan Talaud, yang secara biogeografi diapit oleh Sulawesi, Kepulauan Filipina, dan Kepulauan Maluku, setelah daftar yang pertama dipublikasikan 80 tahun yang lalu. Laporan kami mencakup koleksi amfibi dan reptil yang berasal dari Pulau Salibabu, yang merupakan pulau terbesar kedua di Kepulauan Talaud yang sampai saat ini kurang dikenal dibandingkan dengan daerah lain di sekitar Sulawesi. Di antara koleksi kami yang berjumlah total 37 spesimen, termasuk di dalamnya adalah 3 jenis amfibi dari kelompok Anura, 4 jenis Cicak, 4 jenis Kadal, 2 jenis Londok, dan 1 jenis Biawak. Enam (6) jenis di antara koleksi kami ini baru pertama kalinya dilaporkan dari Kepulauan Talaud, yaitu 1 jenis katak Mikrohila (*Callulops* cf. *dubius*), 2 jenis Cicak (*Nactus* cf. *pelagicus* dan *Gehyra mutilate*), 1 jenis Kadal (*Eutropis* cf. *rudis*), dan 2 jenis Ular (*Typhlops* sp. dan *Boiga irregularis*). Catatan baru dari Pulau Salibabu adalah *Hydrosaurus* sp., *Cyrtodactylus* cf. *jellesmae*, *Eutropis multicarinata* and *Emoia atrocostata*. Kami juga menambahkan *Hemidactylus frenatus* dan *Eutropis multifasciata* ke dalam daftar kami, karena kedua jenis ini dilaporkan telah ditemukan di Kepulauan Talaud dalam daftar online MCZ. Laporan mengenai *Gekko vitattus* yang berasal dari Kepulauan Talaud kemungkinan kurang tepat, namun dapat dibenarkan bila didasarkan pada pola persebaran biografi amfibi dan reptil di daerah Australopapua yang kami ulas dalam tulisan ini. Selanjutnya, laporan tentang ditemukannya *Candoia* di bagian utara Sulawesi kurang dapat dibenarkan. Sampai saat ini, secara keseluruhan tercatat 27 jenis amfibi dan reptil dari Kepulauan Talaud, yang mencakup 3 jenis Katak, 5 jenis Cicak, 8 jenis Kadal, 3 jenis Londok, satu jenis Biawak, dan 5 jenis Ular, di samping 1 jenis Penyu dan 1 jenis Buaya. Seluruh catatan mengenai hewan-hewan ini kami susun dalam sebuah daftar beserta keterangan tambahannya.

Kami juga memaparkan keterlibatan Kepulauan Talaud dalam jalur persebaran amfibi dan reptil yang telah terjadi di antara Pulau Sulawesi, Kepulauan Filipina, dan Kepulauan Maluku dan membandingkannya dengan jalur persebaran organisme lain di daerah ini.

Kata kunci. Wallacea, Sulawesi, amfibia, reptilia, biogeografi, jenis endemik.

1. INTRODUCTION

The Talaud Archipelago represents the northern most area within the Wallacea transition zone between the Oriental and Australian faunal regions. The remote island group lies in the northern Molucca Sea between North Sulawesi, Mindanao in the southern Philippines, and Halmahera in the northern Moluccas. The Talaud Archipelago comprises three main islands: Karakelong, Salibabu and Kaburuang (Fig. 1). Geologically, the Molucca Sea Plate with its inverted U-shape dips east under Halmahera and west under the Sangihe Arc (McCaffrey et al. 1980). The Talaud Islands are situated on the Sangihe forearc separated by a deep ocean trench from the largely submarine Sangihe Arc with its few emergent volcanic islands like Sangihe and Siau (Hall 2002). The Talaud Island group consists of a sedimentary sequence of Middle Miocene to Pleistocene age and includes probable mid-Miocene volcanic rocks and volcaniclustic turbidites (Moore et al. 1981). Pleistocene coral limestone, the youngest rocks on Talaud, are exposed mostly along the coast lines (Fig. 2), but also at 400–500 m elevation on Kaburuang, showing the significant amount of recent uplift (Moore et al. 1981). The highest elevation of only 650 m above sea level is found on Karakelong Island.

The Talaud Islands together with Sulawesi and other islands of present day central Indonesia belong to a biogeographic transition region called Wallacea (see summaries by Mayr [1944] and Simpson [1977]). Australopapuan and Asian animals meet at the respective outer limits of their distribution. Consequently, in the light of biogeography, the Talaud Islands form the northernmost submerged area of this region. Traditionally, the Talaud Archipelago has been dealt with scientifically with Sulawesi to which it is indirectly connected via the Sangihe Island arch. However, the direct over-water distance to North Sulawesi of about 300 km is significantly more distant than Halmahera in the Moluccas (ca. 210 km) or Mindanao in the Philippines (ca. 170 km).

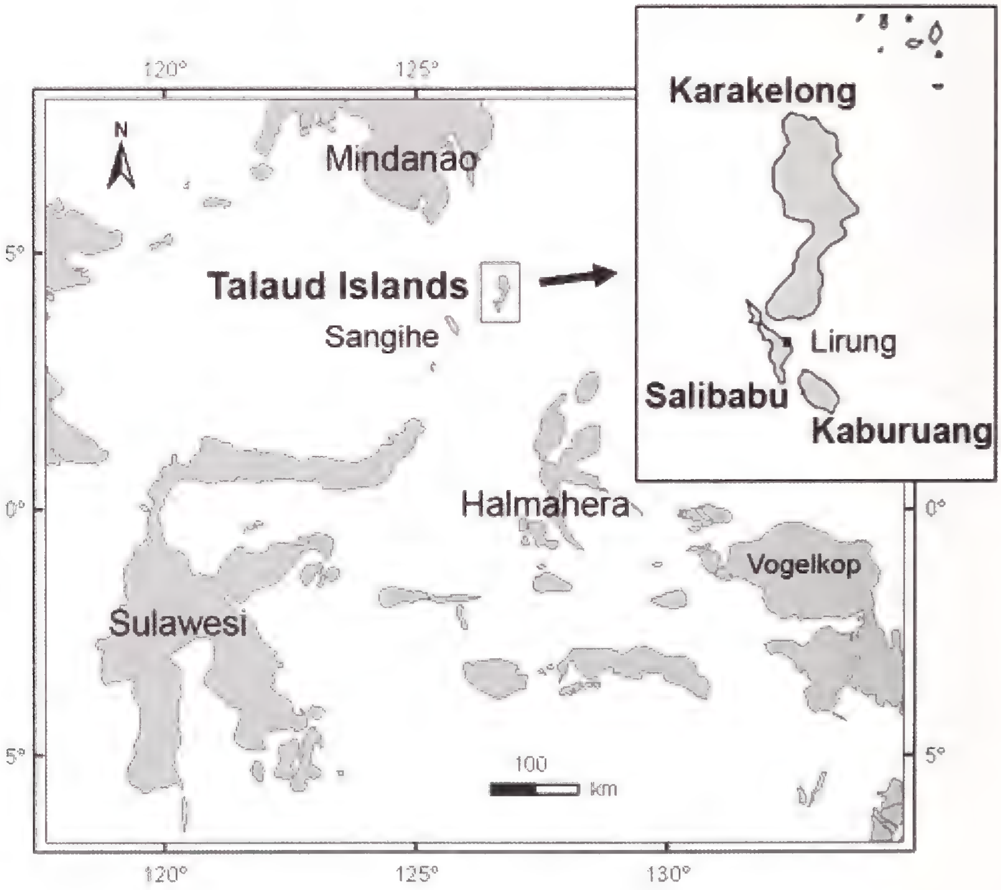

Fig. 1. Map of the Talaud Islands located between Sulawesi, Halmahera (Moluccas) and Mindanao (Philippines).

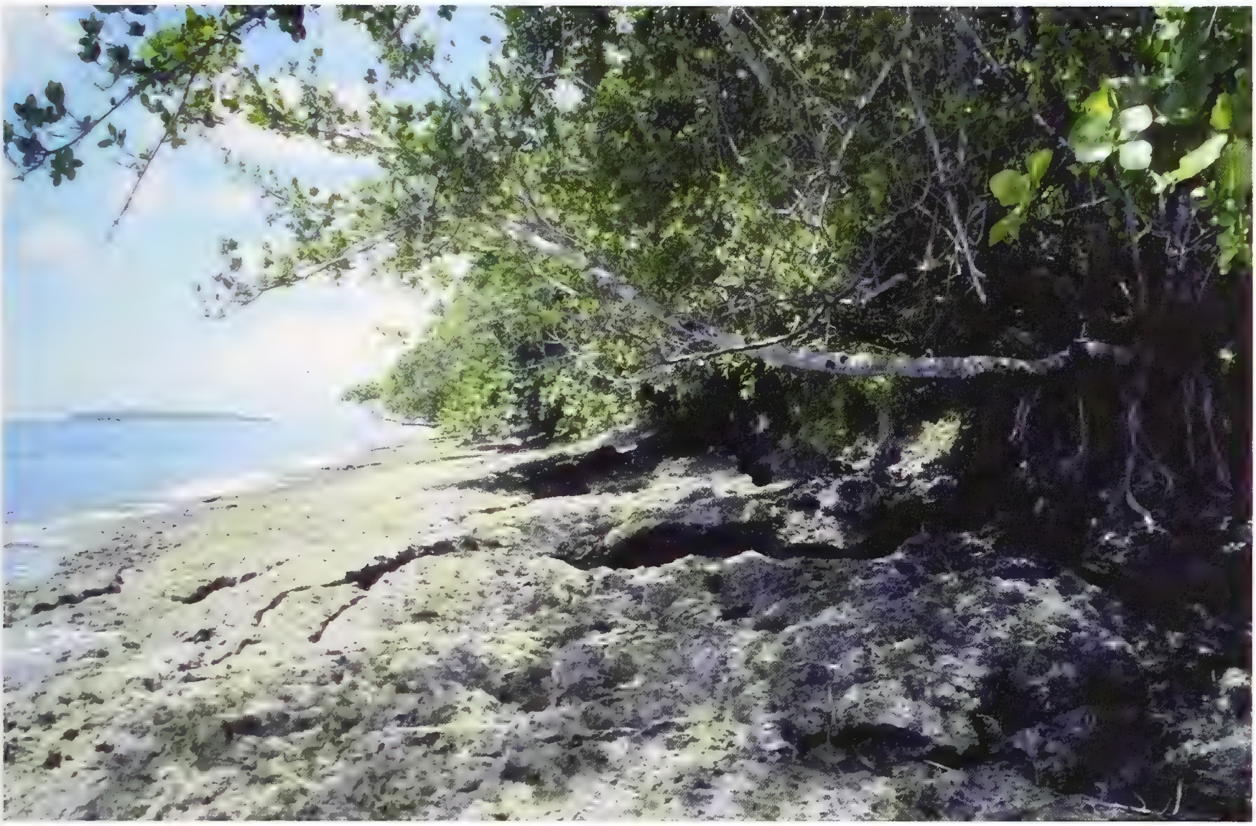

Fig. 2. Coast line with coral limestone deposits on Salibabu Island. Habitat of *Varanus* sp. and *Emoia a. atrocostata*. Photo by André Koch.

The geographically isolated position between three biogeographic subregions in the centre of the Indo-Australian Archipelago render the Talaud Islands an interesting field of research for biogeographers. Until recently, however, the Talaud Archipelago (together with Sangihe) has been one of the least-known areas of the Sulawesi region as defined by VANE-WRIGHT (1991). Hence, due to their minor geographic size together with their remote location, the Talaud Island group has been paid only little attention by herpetologists in the past and scientific literature about the herpetofauna of this small archipelago is scarce. VAN KAMPEN (1907; 1923) and DE ROOIJ (1915; 1917) provided the first herpetological data about the Talaud Islands based on material collected by M. WEBER during the Siboga Expedition of 1899. DE ROOIJ (1915; 1917) listed five different lizards species (*Calotes jubatus*, *Varanus indicus*, *Lygosoma cyanurum*, *Lygosoma rufescens*, and *Mabuia multicarinata*) and one snake species (*Candoia carinata*). Later, DE JONG (1928) published the results of another small collection by the Dutch botanist H. J. LAM who visited Karakelong and Salibabu as well as Miangas, a small islet south of Mindanao, in 1926 (LAM 1926; 1942). His Talaud collection comprised ten different species representing eight lizards and two snakes. Voucher specimens by M. WEBER and H. J. LAM from the Talaud Islands are mostly deposited in the Zoological Museum of the University of Amsterdam. A few of their specimens are stored in the herpetological collection of the Museum Zoologicum Bogoriense (MZB) on Java. Further material (e. g., collected by the Snellius Expedition in 1930) are located in the collections of the Natural History Museum Naturalis in Leiden (RMNH), the Netherlands.

The herpetology department of the Museum of Comparative Zoology (MCZ), Harvard University, houses a small number of vouchers (MCZ R–45768–775; MCZ A–24288) from Karakelong Island collected by the first FAIRCHILD Tropical Botanic Garden Expedition led by the late David FAIRCHILD (1869–1954). This expedition made a short stop-over at the Talaud Islands from 12 to 13 June 1940. The collection merely contains nine specimens representing five lizard species (*Bronchocela cristatella*, *Emoia caeruleocauda*, *Hemidactylus frenatus*, *Lipinia noctua*, and *Eutropis m. multifasciata*) as well as one snake (*Candoia paulsoni tasmai*) and one hylid frog species (*Litoria infrafrenata*). To our knowledge, only MCDOWELL (1979), BROWN (1991) and SMITH et al. (2001) referred, in part, to the FAIRCHILD collection. Therefore, these voucher specimens are included in our report.

This checklist of the Talaud Islands summarizes the present-day knowledge of the herpetofauna and discusses the biogeographic relations and implications of these data. It is the first updated account of the amphibians and reptiles of this remote oceanic archipelago since 80 years.

2. MATERIAL AND FIELD WORK

Field studies on the east coast of Salibabu Island (ca. 95 km^2) were conducted by AK and EA from 13 to 21 July 2005. Collections and observations were made in the vicinity of Lirung, a settlement with a ferry landing stage. Field numbers are AK039 to AK075. The surroundings near the coastline are dominated by agricultural vegetation, especially coconut (*Cocos nucifera*) and nutmeg (*Myristica fragrans*) plantations (Fig. 3). The island's hilly interior was not intensively surveyed. In the low central hills, however, primary habitats or at least areas of minor disturbance still exist (Fig. 4). As recently recognized by Riley (2002), and unlike the neighboring island Salibabu, large areas of Karakelong Island (ca. 970 km^2) are still forested. Surveys were done throughout all hours of day and early night. Specimens were mainly collected manually and with the assistance of a local villager. Voucher specimens were photographed prior to and after euthanization and preserved in 70 % ethanol. They are deposited in the Zoological Museum in Bogor (MZB). Tissue samples of monitor lizards were taken for molecular investigations and preserved in 95 % ethanol. Photographic vouchers are deposited in the private photo collections of AK and EA.

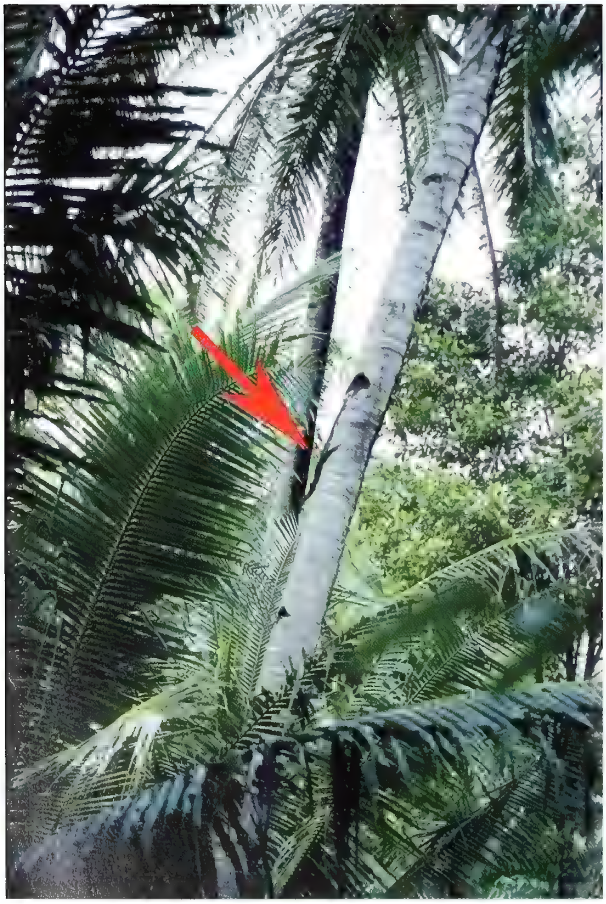

Fig. 3. Coconut and nutmeg plantations dominate the cultivated coastal landscape of Salibabu Island. Red arrow indicates *Varanus* sp. basking on a palm trunk. Photo by André Koch.

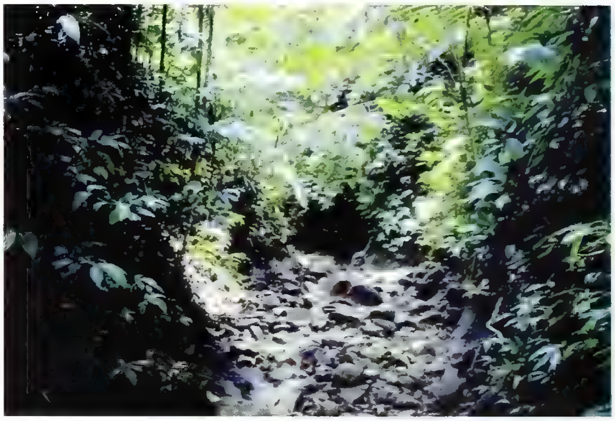

Fig. 4. Undisturbed riverine habitat upcountry of Salibabu Island. Habitat of *Limnonectes* sp. and an unidentified snake species. Photo by André Koch.

Species determination and distribution records follow Boettger (1895a, b; 1903), Boulenger (1897), Barbour (1912), de Rooij (1913; 1915; 1917), van Kampen (1923), de Jong (1928), Mertens (1929), Parker (1934), Tanner (1950), Brown & Alcala (1970), Brown & Alcala (1980), Brown (1991), Monk et al. (1997), Hallermann (2005), de Lang & Vogel (2005), and Ziegler et al. (2007). All species known from the Talaud Islands are listed in Table 1. Abbreviations used are: SVL – snout vent length; TL – tail length; TiL – tibia length. Measurements are given in mm. Museum acronyms are as follows: CAS – California Academy of Science, San Francisco, USA (CAS-SU denotes the Stanford University collection [SU], which is also housed in the CAS); MCZ – Museum of Comparative Zoology, Cambridge, USA; MTD – Museum of Zoology (Museum für Tierkunde), Dresden, Germany; MZB – Museum Zoologicum Bogoriense, Cibinong, Indonesia; RMNH – Nationaal Natuurhistorisch Museum Naturalis, Leiden, Netherlands; ZFMK – Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMA – Zoological Museum, University of Amsterdam, Netherlands.

Information about ZMA specimens was taken from the online database at http://ip30.eti.uva.nl/zmawebsite/search-specimens.php.

The website http://collections.oeb.harvard.edu/Herp/ReptSearch.htm provides information on Talaud specimens in the MCZ collections.

3. RESULTS

ANNOTATED CHECKLIST OF THE AMPHIBIANS AND REPTILES OF THE TALAUD ISLANDS

AMPHIBIA

Hylidae

***Litoria infrafrenata* (Günther, 1867)** (Fig. 5)

***Material examined*:** MZB Amph. 11480, 11490, 11492 (AK039-040, AK072)

***Additional material*:** MCZ A-24288, Karakelong, coll. FAIRCHILD Garden Expedition 1940; ZMA 8570 (3 spec.), Lirung, Salibabu, coll. M. WEBER 1899; ZMA 8576 (1 spec.), Beo, Karakelong, coll. M. WEBER 1899.

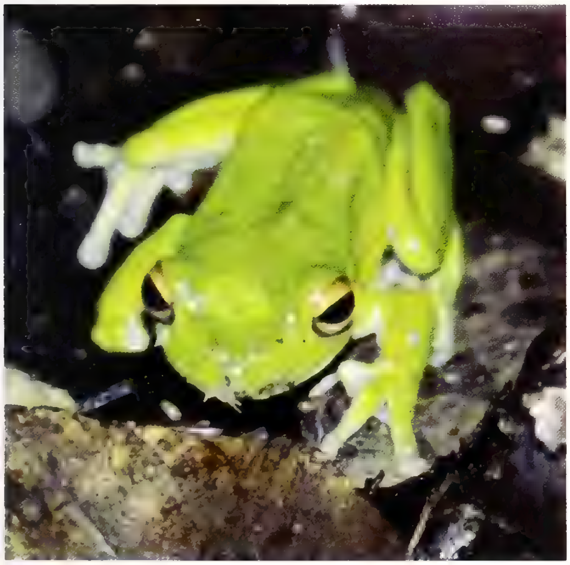

Fig. 5. *Litoria infrafrenata* from Salibabu Island. Photo by André Koch.

Distribution: VAN KAMPEN (1907) was the first to record this species for the Talaud Islands (at that time as *Hyla dolichopsis* Cope, 1867, a junior synonym of *L. infrafrenata*). According to BARBOUR (1912) it "(…) is the most widespread *Hyla* of this whole region [i.e. the Indo-Australian Archipelago]". He listed four female specimens from Lirung and Beo, on Salibabu and Karakelong, respectively. Later however, VAN KAMPEN (1923) only states "Talaut Islands" without specifying the exact locality.

Morphology: VAN KAMPEN (1907) mentioned that disk size varies in this species. Thus, in specimens from Lirung for instance, the disks are smaller than the tympanum (in one specimen three vs. four mm). The same relation applies to our voucher specimens where the disks are also smaller than the eye diameter. SVL of largest specimen (MZB Amph. 11492) 115.5 mm; TiL: 62 mm. Males exhibit black rugosities on the inner side of the first finger. This is the case in our specimen MZB Amph. 11480.

Microhylidae

Callulops* cf. *dubius (Fig. 6)

***Material examined*:** MZB Amph. 11443 (AK047), MZB Amph. 11469 (AK054), MZB Amph. 11470 (AK053), MZB Amph. 11496 (AK074), MZB Amph. 11500 (AK052).

Distribution: Our findings on Salibabu Island expand the known range of the genus by approximately two hundred kilometers to the north and represent a new family record for the Talaud Islands.

Ecology: Subadult and adult voucher specimens were either found in small holes near the base of trees (Fig. 6), or after rainfall near a small stream in the early evening hours (7.30–8.30 pm).

Morphology & Taxonomy: Characteristically short-snouted, small frogs with short limbs: SVL 23.0–39.6 mm, TiL 9.5–15.5 mm; dorsally uniform dark brown to gray-

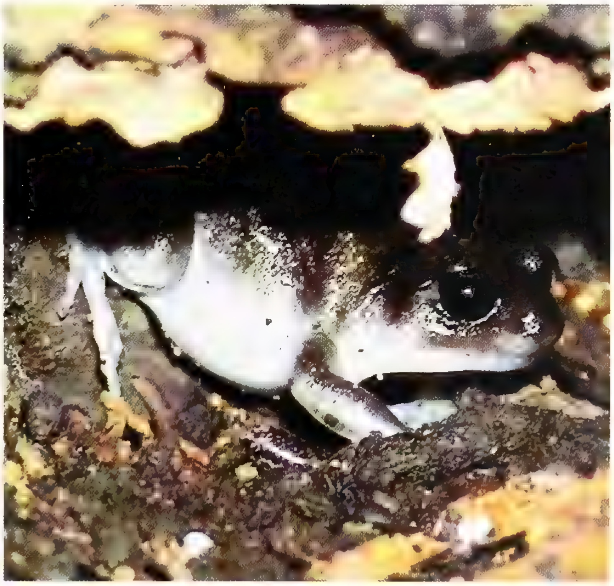

Fig. 6. *Callulops* cf. *dubius* from Salibabu Island. Photo by André Koch.

ish black, ventral side either uniform light grey or dark grey with more or less light mottling, toes with weak light transverse bands.

The Talaud population may represent a member of the *Callulops* (*Phrynomantis*) *robustus* group (R. Günther, pers. comm.). The genus *Callulops* inhabits the Moluccas, New Guinea and surrounding island groups with 17 recognized species (Frost 2007), two of which (*C. boettgeri* and *C. dubius*) are found on Halmahera. According to Méhely (1901) and Parker (1934) *C. boettgeri* is characterized by large triangular discs at fingers and toes, while those of the fingers are larger than those of the toes. Having the finger tips pointed and those of the toes slightly enlarged, fingers and toes without webbings, no maxillary teeth, a smooth skin above and beneath, the nostril much closer to the tip of the snout, tympanum feebly distinct and about half the diameter of the eye, presence of a supratympanic fold (but absent in MZB Amph. 11443 and 11500, possibly due to preservation), our voucher specimens resemble more the second *Callulops* species known from Halmahera, *C. dubius* (Boettger 1895b). However, in contrast to the latter species, the first finger is longer than the second in the Talaud specimens. It cannot be ruled out that the Talaud specimens represent two distinct species due to their differences in ventral color pattern and the presence or absence of a supratympanic fold.

Ranidae

Limnonectes cf. *modestus* (Boulenger, 1882)

***Material examined*:** MZB Amph. 11478 (AK073), 11493 (AK068), 11494 (AK050), MZB Amph. 11497 (AK051).

***Additional material*:** Probably ZMA 8870 (5 spec.), "Taloek, island North of Halmaheira" (= Talaud?!), coll. M. Weber 1900

Distribution: Based on material collected by the Siboga Expedition of Max Weber (six specimens according to van Kampen [1907], but only five according to the ZMA online catalogue; see 'additional material'), van Kampen (1907) was the first to record *L. modestus* from the Talaud Islands without indicating the exact locality. This species is also known from North Sulawesi, the type locality, and some islands in the Moluccas. The Philippine populations have been removed from the synonymy of *L. modestus* (Inger 1954).

Ecology: While two adult voucher specimens were collected near a small stream in the vicinity of the village Lirung, the third (MZB Amph. 11493) was found as road kill next to a coconut plantation.

Morphology & Taxonomy: All three adult specimens closely resemble in morphology and coloration. SVL 58.6–63.6 mm, TiL 32.7–33 mm, head as broad as long or broader than long; vomerine and maxially teeth present; nostril nearer to tip of snout than to eye; tympanum distinct, 3/4 the diameter of the eye; strong supratympanic fold; finger tips pointed, those of the toes with very small discs; first finger slightly longer than second; fingers without webbings, toes nearly fully webbed; dermal fringe along the outer side of fifth toe present; inner palmar tubercle swollen, outer missing; inner metatarsal tubercle present, outer missing; skin smooth without ridges or tubercles. Coloration dorsally olive-green to brownish with little dark spots; tympanum partly blackish; supratympanic fold above tympanum black; upper lips with dark vertical bars; limbs without dark cross bars; posterior part of thighs blackish with orange marbling; ventral side either unicolored whitish cream under head and chest, limbs and posterior half of venter orange, particularly towards vent (MZB Amph. 11494), or underside whitish with grey mottling under head and many grey spots and blotches on chest and venter. Probably three females were collected without vocal sacs. Accordingly, the specimens lack bony processes in the lower jaw as typical for males of *L. modestus*. A fourth subadult specimen of *Limnonectes* was collected in a narrow gorge with a small riverine (Fig. 4). SVL 27.3 mm, TiL 13.8 mm, head slightly longer than broad. Morphologically, this specimen resembles the three adult specimens, except for the indistinct supratympanic fold. However, it shows differences in color pattern. Thus, the dorsal side is brown with distinct darker cross bars and blotches on the limbs; a dark cross bar between the eyes is present, too; the distinct marbling on the posterior part of the femurs is missing.

Menzies (1987) suggested that populations of Sulawesi and Ceram might represent different taxa. Further investigations, morphologically and genetically, are needed to clarify the taxonomic identity of the Talaud populations.

SAURIA

Agamidae

Bronchocela cristatella (Kuhl, 1820) (Fig. 7)

***Material examined*:** MZB Lac. 5080 (AK057).

***Additional material*:** ZMA 18832 (4 spec.), Gunung Doeata (= Mt. Duata), Karakelong, coll. H. J. Lam, 1926; ZMA 18833, Lirung, Salibabu, coll. H. J. Lam, 1926; MCZ R-45770, -771, Karakelong, coll. Fairchild Garden Expedition, 1940

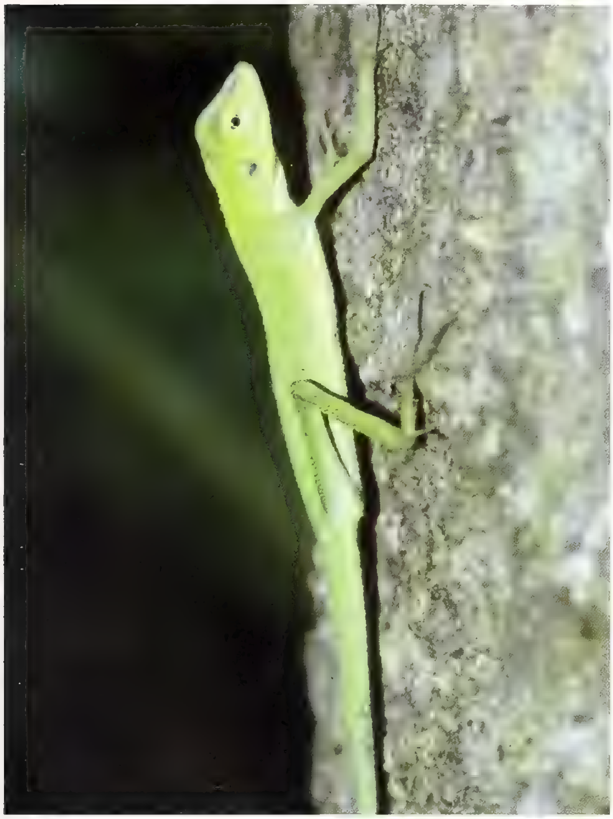

Fig. 7. *Bronchocela cristatella* from Salibabu Island. Photo by André Koch.

Distribution: De Jong (1928) reported that H. J. Lam collected several specimens of *B. cristatella* on Karakelong and Salibabu Island. Two further specimens were collected by the Fairchild Expedition in 1940. As neither of these old voucher specimens has been included in a recent review of the genus *Bronchocela* (Hallermann 2005), their taxonomic identification requires verification. Nevertheless, our investigations confirm that *B. cristatella* also inhabits the Talaud Archipelago next to Sulawesi, the Philippines and the Moluccas.

Ecology: The voucher specimen (MZB Lac. 5080) was found on a tree trunk near three small fish ponds where *Hydrosaurus* also occurred. Another subadult specimen of *Bronchocela* was discovered sitting on a thin branch above a small stream near Lirung village.

Morphology: SVL 89 mm, TL 298 mm (TL/SVL: 3.34); eight supralabials; nine infralabials; 55 scales around midbody, the first five to six upper scale rows of the lateral side keeled and pointing upwards; ventral scales larger than dorso-laterals; 35 strongly keeled scales under fourth toe; six to seven scales along canthus rostralis between nostril and anterior border of orbit; diameter of tympanum more than half diameter of orbit (0.83).

***Bronchocela jubata* Duméril & Bibron, 1837**

***Material examined*:** none

***Additional material*:** ZMA 18866, Lirung, Salibabu, coll. M. Weber 1899; ZMA 18869, Beo, Karakelang (= Karakelong), coll. M. Weber 1899.

Distribution & Taxonomy: Because Hallermann (2005) did not examine the ZMA specimens collected by Weber, he stated that older records of *B. jubata* from the Talaud Islands by de Rooij (1915) may be correct. However, 14 specimens from Sulawesi formerly deposited in the Leiden collection (RMNH 3021a-e, 3023a-d, and 7419a-e) as *B. jubata*, were redetermined by Hallermann (2005) as *B. celebensis*, which is endemic to Sulawesi. In turn, three older records of *B. jubata* from Sulawesi in the Berlin collection (ZMB) are correct according to this author. From the entire Philippine Archipelago only one voucher specimen from Mindanao (ZMB 16305) was included in the review by Hallermann (2005). Four further specimens (ZMB 34117) allegedly from the Philippines lack specific locality data. Thus, it remains uncertain if two different species of *Bronchocela* live in sympatry on the Talaud Islands. Pending molecular genetic studies and further field work will hopefully reveal the systematics and the exact distributions of these morphologically diverse agamids.

***Hydrosaurus* sp.** (Fig. 8)

***Material examined*:** MZB Lac. 5081 (AK049).

Distribution: De Jong (1928) reported *Hydrosaurus amboinensis* for Karakelong Island. This is the first record of this large agamid for Salibabu Island.

Ecology: During recent field surveys on Salibabu Island three adult specimens were flushed out. One female specimen was observed sitting on a tree with remarkable thin branches. One juvenile voucher specimen was encountered near a small fish pond. On Talaud, *Hydrosaurus* displays a cryptic life style and seems to avoid the coast line. This agamid species prefers less anthropogenically influenced inland habitats with freshwater environment.

Morphology: SVL 116.5 mm, TL 243 mm; tympanum diameter 3.1 mm; dorsal crest missing, nuchal crest indicated by a row of 16 prominent scales; six to seven interocularia; 11 supralabials, sixth to eleventh under eye; 11 infralabials; mental large; one row of six and seven enlarged submaxillaries, respectively, separated from infralabials by one (first IL) or several small scales; lateral scales heterogeneous, mainly small and strongly carinate, interspersed

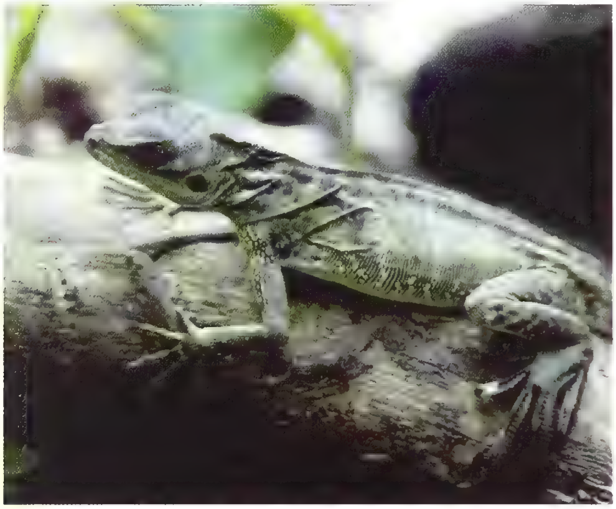

Fig. 8. *Hydrosaurus* sp. from Salibabu Island. Photo by André Koch.

with six groups of two to six tubercular, carinate scales; three further such enlarged scales along the side of the neck; towards the ventral side numerous enlarged, smooth scales arranged in more or less distinct transverse rows; ventral scales homogenous, smooth; subdigitals under fourth toe small at basis, followed by 35 relatively enlarged subdigitals after first phalanx; toes laterally with a row of extremely wide (up to 1.9 mm) scales, 36 at fourth toe forming a serrated edge. Ten and eleven femoral pores, respectively. Ground color green to brownish with enlarged scales of the dorsal and lateral side being lighter; ventral side whitish, throat darker.

Taxonomy: Phenetically, the Talaud specimen resembles a juvenile *H. pustulatus* from Panay Island, central Philippines, in color pattern and scalation (photo courtesy of M. Gaulke). However, a systematic assignment of the Talaud population either to *H. amboinensis* from Sulawesi, *H. pustulatus* from the Philippines, *H. weberi* from Halmahera or to another hitherto unrecognized taxon seems premature at this time, due to the lack of diagnostic characters (dorsal and nuchal crests, adult color pattern) in the juvenile voucher specimen and insufficient material for comparison of the three *Hydrosaurus* taxa currently recognized.

Gekkonidae

Cyrtodactylus cf. *jellesmae* (Boulenger, 1897)

***Material examined*:** MZB Lac. 5126 (AK056), MZB Lac. 5128 (AK055).

Additional material: ZMA 15942 (1 spec.), Gunung Doeata (= Mt. Doata), Karakelong, coll. H. J. LAM 1926; ZMA 17884 (1 spec.), same data as previous specimen.

Distribution: DE JONG (1928) reported one specimen (but see 'additional material') of *C. marmoratus* from Karakelong Island. However, BRONGERSMA (1934) showed that Sulawesi specimens of *C. marmoratus* were referable to *C. fumosus*. Accordingly, ISKANDAR & NIO (1996) doubted the occurrence of *C. marmoratus* on Sulawesi as previously mentioned (e.g., DE ROOIJ 1915). This is the first record of *C.* cf. *jellesmae* for Salibabu Island and the northernmost occurrence of the entire range of this species.

Ecology: Both voucher specimens, apparently a female and a male (the female carrying two well-developed eggs which are visible through the thin skin), were found at 20.30 p.m. at low elevations on the trunks of a tree and a coconut palm, respectively.

Morphology: Both sexes lack preanal and femoral pores and the ear openings are oval as characteristic for *C. jellesmae* (BOULENGER 1897; DE ROOIJ 1915). Lateral fold present between axilla and groin. However, in coloration and scalation the Salibabu population differs from those of Sangihe Island and north Sulawesi. The characteristic dark, V- and M-shaped dorsal markings are less distinct and the tubercles have light tips only laterally. In addition, the Talaud population shows less pronounced tubercles on dorsum, legs and tail. From the new described species, *C. wallacei*, the Talaud geckos are distinguished by the absence of enlarged subcaudal scales (HAYDEN et al. 2008).

Taxonomy: Probably DE JONG's (1928) specimen from the Talaud Islands will prove to belong to *C.* cf. *jellesmae* which was frequently found on Sulawesi and adjacent islands compared to *C. fumosus* and *C. wallacei* (unpubl. data). Future molecular studies are required to enlighten the systematics and taxonomy of this morphologically cryptic complex of gecko species in the Sulawesi region.

Gehyra mutilata (Wiegmann, 1834)

***Material examined*:** MZB Lac. 5124 (AK046).

Distribution: *Gehyra mutilata* is herein reported for the first time for the Talaud Islands. This invasive gecko species inhabits Southeast Asia, Oceania, Madagascar, Mexico, California, Hawaii, and New Zealand. It was probably accidentally introduced from the Philippines or North Sulawesi by human transportation.

Ecology & Morphology: The voucher specimen, a female containing two eggs, was collected on the wall of a house in Lirung village where several specimens were observed. SVL 50 mm, TL 53 mm.

Gekko vittatus Hottuyn, 1782

***Material examined*:** none

Distribution: In the distribution table of "East Indian" herptiles, BARBOUR (1912: 179) listed the Talaud Islands within the range of *Gekko vittatus*. This gecko species is known from the Moluccas, New Guinea and surrounding archipelagos. Thomas BARBOUR himself did not visit the Talaud Islands but he was aware of VAN KAMPEN's (1907) account about amphibians based on Max WEBER's collections from that island group. The correctness of BARBOUR's (1912) data cannot be proven as no information on voucher specimens was provided. Theoretically, however, the occurrence of this gecko species on the Talaud Archipelago seems possible as other Australopapuan species also inhabit this island group. Future investigations in the herpetofauna of the Talaud Islands may answer this question.

Hemidactylus frenatus Duméril & Bibron, 1836

***Material examined*:** none

Additional material: MCZ R-45768, and R-45769, Karakelong, coll. FAIRCHILD Expedition 1940.

Distribution & Ecology: This circum-tropically distributed gecko species was frequently seen on walls of houses. Our observations suggest that *H. frenatus* and *G. mutilata* are more common on Talaud than on neighboring Sangihe Island. Two voucher specimens (see 'additional material') of the FAIRCHILD Expedition are deposited in the MCZ collection.

Nactus pelagicus complex (Fig. 9)

***Material examined*:** MZB Lac. 5086 (AK075).

Ecology: During daytime one specimen was found under a rotten tree trunk in a hilly area near Lirung on Salibabu Island.

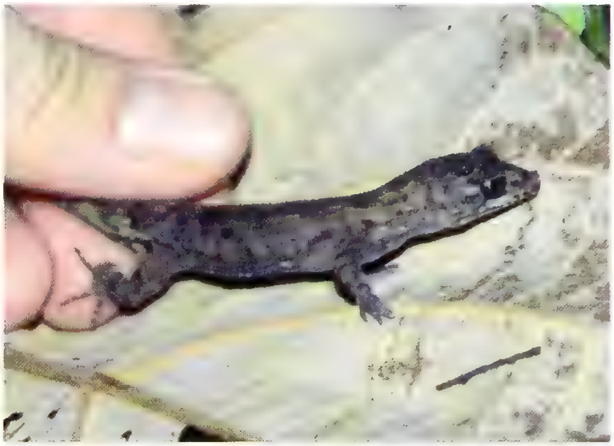

Fig. 9. *Nactus* cf. *pelagicus* from Salibabu Island. Photo by André Koch.

Morphology: SVL 54 mm; tail regenerated, 55 mm long, fifth toe of left hind limb missing; probably a female, preanal pores missing; dorsum, limbs and tail (except for regenerated part) covered with granules and conical tubercles forming six regular longitudinal rows on the back, irregularly arranged along the lateral sides; rostral large; only 5 supralabials (as compared to other populations); 7 infralabials; mental large, a pair of small chin-shields posterior to the mental; ventral side covered with small granulous scales; 19 subdigits under fourth toe. Coloration of dorsal side dark brown with blackish blotches on the back, increasing in number towards the snout, labial sutures whitish; ventrally dark grayish-brown, regenerated tail with irregular light markings.

Distribution & Taxonomy: This is the first record of the genus *Nactus* for the Talaud Islands representing the northern most population of this widespread Pacific species group which is known to consist of bisexual and parthenogenetic species (MORITZ 1987; DONNELLAN & MORITZ 1995; ZUG 1998). The taxonomic status of most New Guinean population is still uncertain (KRAUS 2005; JACKMAN et al. 2008). Traditionally, they have been assigned to *N. pelagicus* and *N. vankampeni*, but unisexual *N. pelagicus* have been shown to be restricted to southern Vanuatu, New Caledonia, and Oceania (ZUG & MOON 1995). TANNER (1950) reported a specimen from Morotai close to Halmahera which was obviously a male because it "(…) has an angular series of 7 preanal pores".

Scincidae

Emoia a. atrocostata (Lesson, 1826) (Fig. 10)

***Material examined*:** MZB Lac. 5130 (AK071).

***Additional material*:** RMNH 18659, Karakelong, coll. Snellius Expedition (Dr. H. BOSCHMA), 14–21 June 1930.

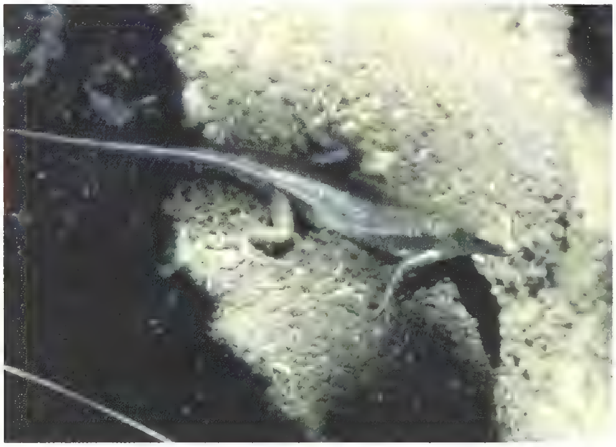

Fig. 10. *Emoia a. atrocostata* from Salibabu Island. Photo by André Koch.

Distribution: According to BROWN (1991) the Talaud population of *E. atrocostata* belongs to the nominotypic subspecies. He examined one specimen from Karakelong (RMNH 18659). This coastal skink species is widespread ranging from the Philippines through the Indo-Australian Archipelago and many Pacific island groups such as the Carolines and Palau reaching North Australia. This is the first record of *E. a. atrocostata* for Salibabu Island.

Ecology: The voucher (MZB Lac. 5130), a weak adult specimen infested with several red mites (Acari), was resting on coral limestone with temporary ponds at the shoreline where this species was frequently found on Salibabu Island (Fig. 2). Early activity was observed at 7 a. m. although the sky was cloudy and temperatures were relatively low.

Morphology: SVL 85.4 mm, tail short, laterally compressed, 73.6 mm long; TL/SVL 0.86; seven supralabials, fifth enlarged and below eye; tympanum small; lower eyelid with a transparent disk; one pair of nuchals; 38 midbody scale rows; 33 rounded lamellae under fourth toe.

Emoia caeruleocauda (de Vis, 1892)

***Material examined*:** MZB Lac. 5114 (AK043), MZB Lac. 5115 (AK041), MZB Lac. 5118 (AK042), MZB Lac. 5127 (AK069).

***Additional material*:** MCZ 45774, coll. FAIRCHILD Expedition, 1940; ZMA 18384 (1 spec.), Liroeng (= Lirung), Salibabu, coll. M. WEBER 1899; ZMA 18391 (as *Lygosoma triviale*; 2 spec.), Beo, Karakelong, coll. H. J. LAM 1926; ZMA 18392 (as *Lygosoma triviale*; 5 spec.), Gunung Doeata (= Mt. Doata), Karakelong, coll. H. J. LAM 1926; ZMA 18395 (as *Lygosoma triviale*), Liroeng (= Lirung), Salibabu, coll. H. J. LAM 1926; ZMA 18409 (as *Lygosoma triviale*; 1 spec.), Beo, Karakelong, coll. M. WEBER 1899.

Distribution & Taxonomy: The Talaud population was formerly recognized as *E. cyanura* (DE ROOIJ 1915; DE JONG 1928), which in contrast to *E. caeruleocauda* is widely distributed in Pacific islands from the Bismarck Archipelago eastwards (BROWN 1991). BROWN (1991) revised the genus and identified one specimen (MCZ 45774) from Karakelong as *E. caeruleocauda*.

Morphology: According to Brown (1991), these phenetically similar species (*E. cyanura* and *E. caeruleocauda*) can be distinguished by the shape and number of lamellae under the fourth toe. Two specimens from Salibabu (MZB Lac. 5115, 5127) each had 44 lamellae under the fourth toe, thus confirming the occurrence of *E. caeruleocauda* on the Talaud Archipelago. Lower eyelid with a transparent disk; hind limb reaches the axilla.

Ecology: On Salibabu Island *E. caeruleocauda* was frequently found on the ground and low vegetation. It is the most common lizard of the Talaud Archipelago. These conspicuous lizards use their metallic-blue tail fluttering from side to side to distract potential predators, mark male territories and attract potential mates.

Eugongylus rufescens (Shaw, 1802)

***Material examined*:** none

***Additional material*:** ZMA 12491 (4 spec.), Gunung Doeata (= Mt. Duata), Karakelong, coll. H. J. LAM 1926; ZMA 12492 (1 spec.), Lirung, Salibabu, coll. M. WEBER 1899

Distribution: DE ROOIJ (1915) listed *Eugongylus rufescens* for Salibabu Island and DE JONG (1928) reported another specimen of this skink from Karakelong (according to the online ZMA database 4 specimens are summarized under collection number ZMA 12491). We could not find this species during our field work. The Talaud populations represent the most north-western distribution of this short-legged skink which inhabits New Guinea, the Solomon and Admiralty Islands finally reaching northern Australia.

Eutropis m. multicarinata (Gray, 1845) (Fig. 11)

***Material examined*:** MZB Lac. 5084 (AK063), MZB Lac. 5085 (AK062), MZB Lac. 5087 (AK061), MZB Lac. 5116 (AK060), MZB Lac. 5117 (AK058).

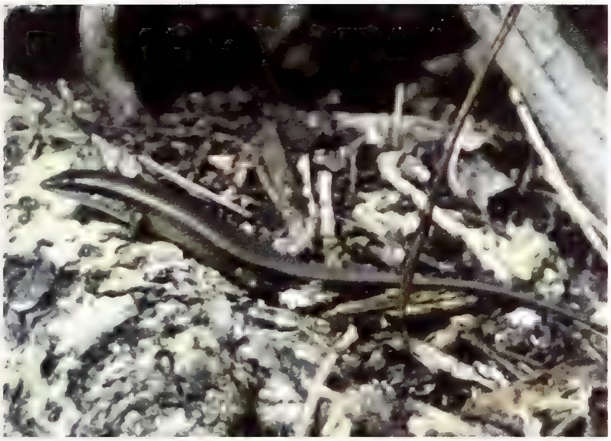

Fig. 11. *Eutropis m. multicarinata* from Salibabu Island. Photo by André Koch.

***Additional material*:** ZMA 18454 (1 spec.), Beo, Karakelong, coll. M. WEBER 1899.

Distribution: DE ROOIJ (1915) recorded *Eutropis multicarinata* (at that time still in the genus *Mabuya*, but taxonomically partitioned by MAUSFELD et al. [2002]) from Karakelong Island. Our findings represent the first record of this species for Salibabu Island. Thus, on the Talaud Islands *E. multicarinata* has its most south-eastern distribution.

Ecology: Five specimens were collected in the vicinity of Lirung (partly at night, 8.30 p.m.) while resting at the base of a tree. During daytime, brown skinks, though undetermined, climbed up tree trunks when chased. These observations suggest that *E. multicarinata* is adapted to a semi-arboreal life style.

Morphology: According to DE ROOIJ (1915), *E. multicarinata* can be distinguished from the phenetically similar species *E. rudis* and *E. multifasciata* by the absence of postnasal scales and five or seven strong keels on nuchals, dorsals and laterals. According to BROWN & ALCALA (1980) *E. multicarinata* has 22 to 29 lamellae (usually 24-28) beneath the fourth toe, while *E. multifasciata* has only 16 to 21, and *E. rudis* 18 to 22. Furthermore, these authors provide the following scalation data. *E. multicarinata* has 28 to 32 scales around midbody, while *E. multifasciata* has 30 to 34, and *E. rudis* 28 to 32. All specimens match the definitions by DE ROOIJ (1915) and BROWN & ALCALA (1980) in having six or seven keels on dorsals (fused nuchals with up to 11 keels!), 22 to 25 lamellae beneath fourth toe, and 32 to 33 scales around midbody. At least in one specimen (MZB Lac. 5087) the postnasal is absent. However, in MZB Lac. 5084 and MZB Lac. 5085 a postnasal is present. The prefrontals are separated by the frontal. The dorsal side is brown, sometimes interspersed with few darker spots, laterally with a dark brown streak from behind the eyes along the body, sometimes bordered above by a light brown streak; ventral side light yellowish to grey, throat in three specimens bluish-grey; supralabials also grayish. The Talaud population of *E. multicarinata* can be assigned to the nominal subspecies because the parietals are separated by the interparietal. All voucher specimens, however, lack blackish spots or blotches below the head and throat as characteristic for *E. m. borealis* (BROWN & ALCALA 1980).

Eutropis multifasciata (Gray, 1845)

***Material examined*:** none

***Additional material*:** MCZ R-45772 and MCZ R-45773, Karakelong, coll. FAIRCHILD Garden Expedition 1940.

Distribution: *Eutropis multifasciata*, a widespread species known also from Sulawesi, the Philippines and Halmahera in the Moluccas, was not found during this biodiversity survey. However, more than 60 years ago, the FAIRCHILD Garden Expedition collected two specimens (see 'additional material') of this skink on Karakelong which have not yet been reported. We provide here the first record of this skink from the Talaud Island. In addition, H. J. LAM collected this species on Miangas north of the Talaud Islands (DE JONG 1928).

Taxonomy: Although *E. multifasciata* in known to occur sympatrically with its congeners *E. multicarinata* and *E. rudis* on Mindanao in the Philippines (BROWN & ALCALA 1980), the identification of the FAIRCHILD voucher specimens should be re-confirmed due to the observed differences in scalation characters in *E. multicarinata* and *E.* cf. *rudis* (see below).

Eutropis cf. *rudis* (Boulenger, 1887) (Fig. 12)

***Material examined*:** MZB Lac. 5142 (AK044), MZB Lac. 5113 (AK070).

Ecology: Two subadults (MZB Lac. 5142: SVL 36.8 mm, TL 50.0 mm; see Fig. 12) were collected near Lirung on Salibabu Island in a coconut and nutmeg plantation and on the beach, respectively.

Morphology & Taxonomy: To distinguish *E. rudis* from *E. multifasciata*, BROWN & ALCALA (1980) mention that the prefrontals are in broad contact in the latter species while they are usually narrowly separated (or rarely in contact) in *E. rudis*. Aside this scalation character, both voucher specimens largely agree with the definition by BROWN

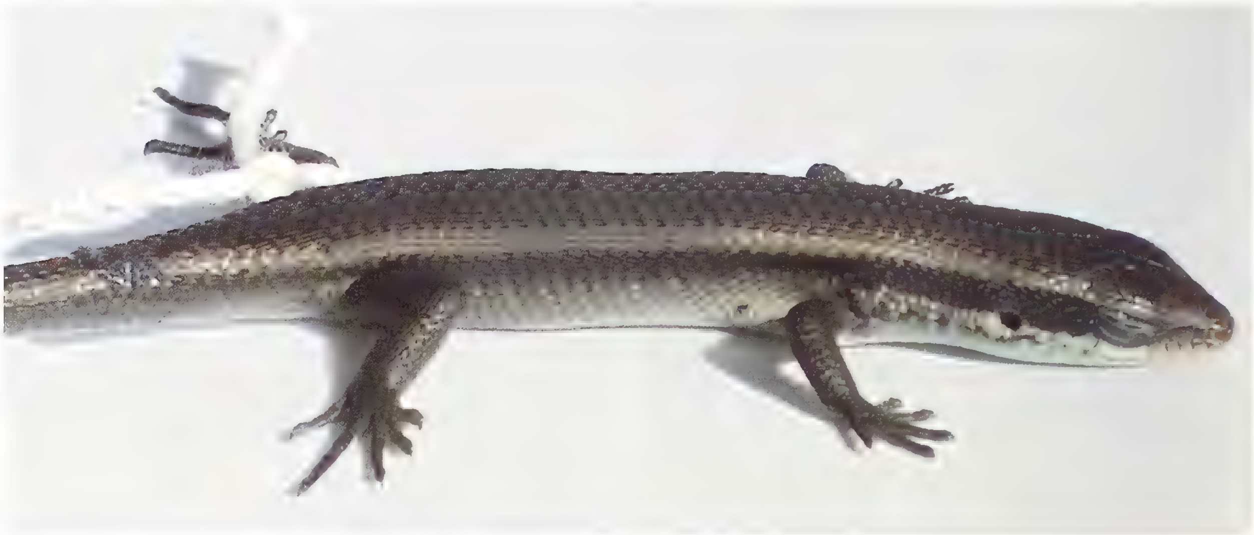

Fig. 12. *Eutropis* cf. *rudis* from Salibabu Island. Photo by André Koch.

& Alcala (1980) in having 20 and 22 keeled lamellae under fourth toe, 32 and 30 midbody scale rows (usually 28–30, rarely 31 or 32; 28–31 in *E. rudis* from Sulawesi according to Howard et al. [2007]), respectively. A postnasal is present. The hind limbs of MZB Lac. 5142 reach the axilla as postulated by de Rooij (1915), while MZB Lac. 5113 exhibits tricarinate dorsals as typical for *E. rudis*. The second specimen's dorsal scales have up to five keels (very rarely in *E. rudis* according to Brown & Alcala [1980]), of which the three medians are strongly pronounced and flanked by two feeble outer keels. The Talaud specimens share this character with the newly described *E. grandis* from Sulawesi (Howard et al. 2007), from which, however, they are clearly distinguishable by higher midbody scale counts (30–32 vs. 25–27 in *E. grandis*). In contrast to Brown & Alcala (1980) and Howard et al. (2007) both vouchers have 40 paravertebral rows (vs. 34–38 in Philippine *E. rudis* and 34–35 in Sulawesian *E. rudis*, respectively) between parietals and base of tail. The dorsal side is brown, laterally with a dark brown streak starting behind the nostrils, bordered above by a light brown streak; ventral side light grey, supralabials also grayish. In specimen MZB Lac. 5113 the ventral side is light gray only on the first half of the body; the rest including hind limbs and tail is brownish.

Because both voucher specimens are not fully grown, the identification as either *E. rudis* or *E. multifasciata* is not unequivocal. Deviations in vertebral scale counts from those provided by Brown & Alcala (1980) may be explained by geographic variation. Therefore, we here preliminarily allocate them to *E.* cf. *rudis*. Further investigations will reveal if *E. rudis* really inhabits the Talaud Islands.

***Lamprolepis smaragdina* ssp. (Lesson, 1830)** (Fig. 13)

***Material examined*:** none

***Additional material*:** ZMA 11304 (1 spec.), Karakelang (= Karakelong), coll. H. J. Lam 1926; ZMA 18231 (1 spec.), Liroeng (= Lirung), Salibabu, coll. H. J. Lam 1926.

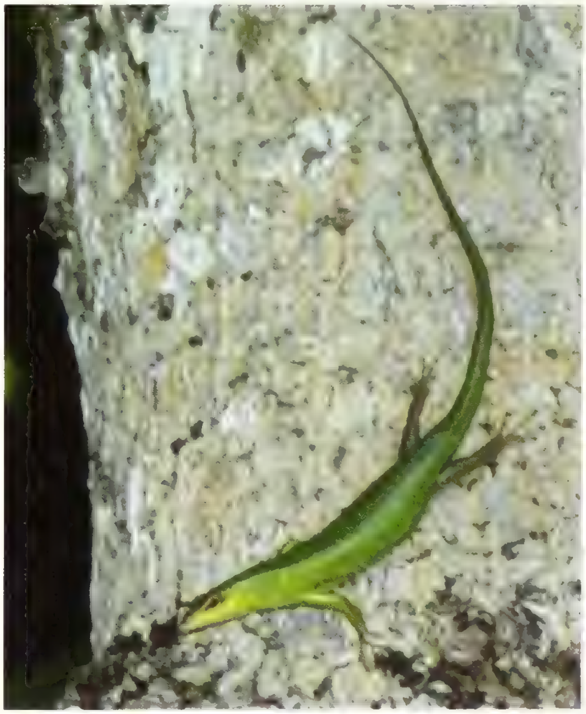

Fig. 13. *Lamprolepis smaragdina* ssp. from Salibabu Island. Photo by André Koch.

Distribution & Taxonomy: De Jong (1928) reported two specimens of *L. smaragdina* from the Talaud Islands. Mertens (1929), who examined de Jong's voucher specimens mentioned that despite their minor geographic distance to the Philippines the Talaud specimens (and even those of the Miangas further north to Mindanao) resemble *L. smaragdina viridipuncta* inhabiting the Pacific archipelagos of Palau, the Carolines, and eastward to the Marshall Islands. Nevertheless, he allocated the Talaud population to the Philippine subspecies *L. s. philippinica*. Mertens (1929) remarked that one specimen from Lirung, Salibabu, was the largest of more than 100 voucher specimens he examined from all over the species' range; its SVL measured 114 mm, and the black markings typical of Philippine populations were largely reduced. This pattern of *L. s. viridipuncta* was also found in the only specimen from Mindanao available to Mertens (1929). He finally designated the Talaud and Miangas populations as a hybrid form of the Philippine and Pacific taxa.

Morphology: Observations and photographs of a few adult specimens active on trees and coconut palms near the coast of Lirung match Mertens' (1929) description of the Salibabu specimen. The uniformly green coloration without any markings is different from populations of *L. smaragdina* on both neighboring islands of Sangihe and north Sulawesi. No specimens of the *viridipuncta* subspecies were examined.

***Lipinia noctua* (Lesson, 1826)**

***Material examined*:** none

***Additional material*:** ZMA 18348, Gunung Doeala (= Mt. Doala), Karakelong, coll. H. J. Lam 1926; MCZ R-45775, Karakelong, coll. Fairchild Garden Expedition 1940

Distribution: The record for Talaud by de Jong (1928) was not mentioned by Zweifel (1979) who examined the variation in the moth skink, *Lipinia noctua*. A second specimen (MCZ R-45775) was collected by the Fairchild Expedition. The Talaud population represents the most northwesterly distribution for this cosmopolitan Pacific species. During our survey we could neither record this species, nor could we examine de Jong's voucher specimen.

Varanidae

***Varanus* sp. (aff. *indicus* Daudin, 1802)** (Figs 3, 14)

***Material examined*:** MZB Lac. 5176 (AK067), MZB Lac. 5177 (AK064), MZB Lac. 5178 (AK059), MZB Lac. 5179 (AK066), MZB Lac. 5180 (AK065); MZB Lac. 581 (954), Karakelong Island, coll. H. J. Lam 1926; MZB Lac. 4195, Beo, Karakelong Island, coll. J. Riley of WCS (World Conservation Society) 9 June 1999; ZMA 15411b, Lirung, Salibabu, coll. M. Weber and Siboga Expedition 25-27 July 1899; ZFMK 87587 (formerly ZMA 15411a), same data as previous specimen.

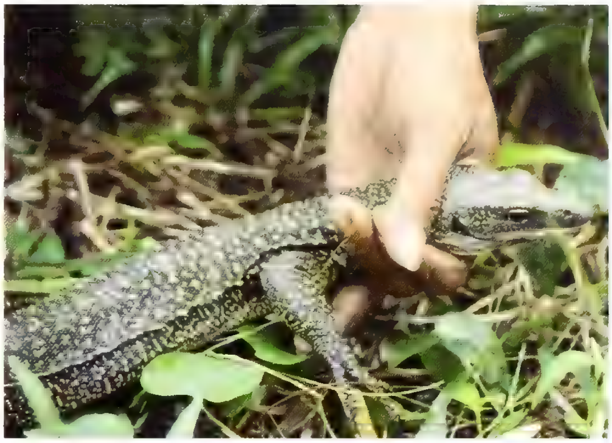

Fig. 14. *Varanus* sp. from Salibabu Island. Photo by André Koch.

Distribution: The Talaud population represents the most north-westerly distribution of a member of the *Varanus indicus* species group (Ziegler et al. 2007). Interestingly, Auffenberg (1980: 109) listed two specimens of *V. salvator* from Liroeng (= Lirung) on Salibaboe (= Salibabu) Island in the collection of the Museum Zoologicum Bogoriense (MZB Lac. 947 and 954, respectively). These vouchers, however, could not be located in the MZB collection. According to the MZB herpetology catalogue, the collection numbers to which Auffenberg (1980) referred belong to a specimen of *V.* cf. *nebulosus* and *V. indicus*, respectively (I. Sidik pers. comm.). The latter was collected by H. J. Lam on Salibabu Island in 1926. Accordingly, we could not confirm a potential co-existence of Pacific monitor lizards with the water monitor, *V. salvator*, on Salibabu Island. Although local people reliably stated that there are two giant reptile species found on the island, the description of the second species fits exactly with the large sailfin lizard, *Hydrosaurus*.

Ecology: On Salibabu Island monitor lizards are frequently found in disturbed and cultivated areas like coconut plantations near the coast line. Thus, a preference for saltwater influenced habitats as reported for *V. indicus* on New Guinea (Philipp 1999) could also be confirmed for the Talaud monitor lizards. Five mature specimens were found during day time on palm or tree trunks while basking or mating (Fig. 3). Only once, a juvenile specimen was flushed out near a runnel but escaped in the dense vegetation. These observations suggest an ecological separa-

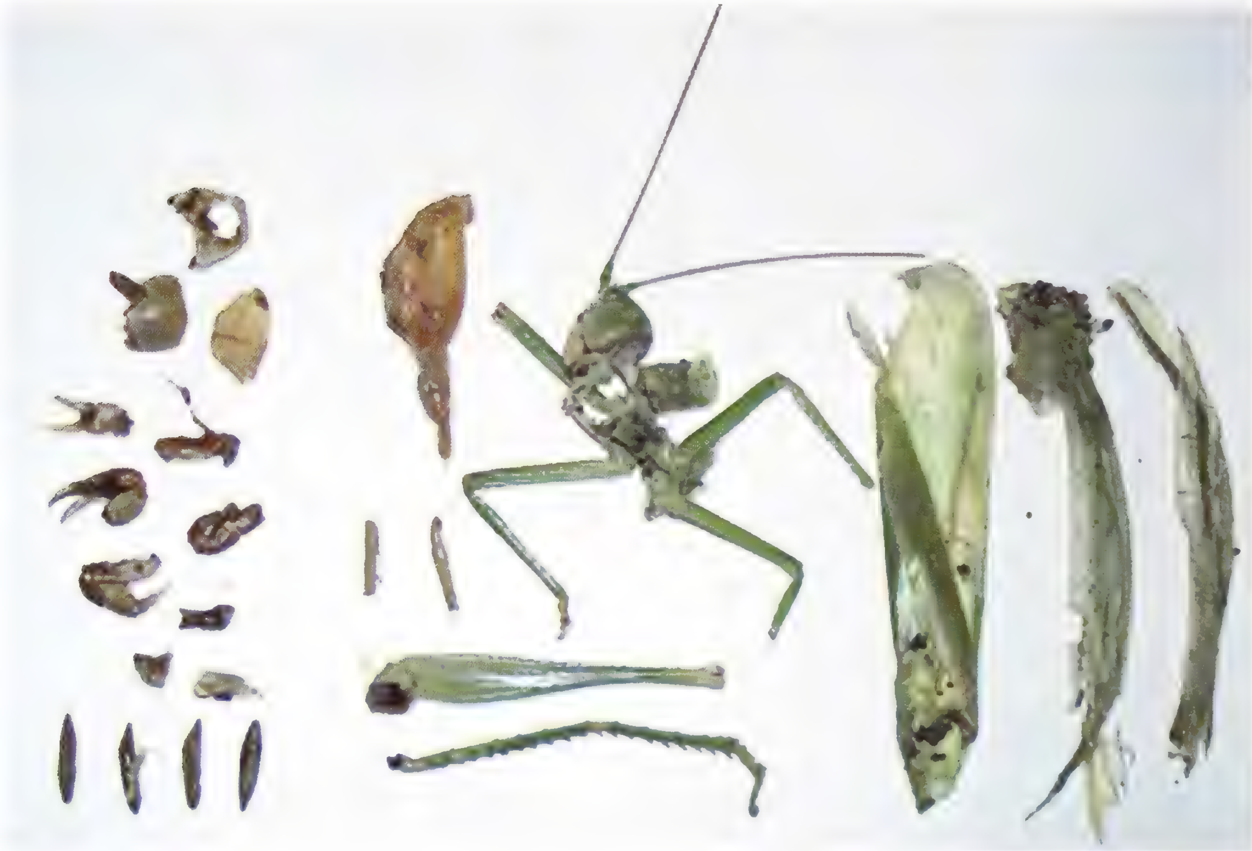

Fig. 15. Defecated prey remains from specimen MZB Lac. 5178 of *Varanus* sp. representing a large orthopteran (*Sexava* sp., Tettigoniidae) and fragments of a crab.

tion of different age groups in the Talaud monitor lizards. While juvenile specimens seem to hide in thicket on the ground, adults obviously prefer a semi-arboreal life. The avoidance behaviour of juveniles seems reasonable because cannibalism is common in many monitor lizard species.

Although monitor lizards are regularly hunted for food supply by local people, no direct threat of the Salibabu population could be recorded. Natural predators are scarce as no large carnivorous mammals are known from these islands (RILEY 2002). However, crocodiles (*Crocodylus* sp.) and the reticulated python (*Python reticulatus*) should be considered natural predators.

Diet: After being caught specimen MZB Lac. 5178 defecated the undigested remains of a small crab and a large green orthopteran (*Sexava* sp., Tettigoniidae) (Fig. 15). Furthermore, the stomach of ZFMK 87587 contained a well-preserved specimen of a large spider ("*Olios*" *coccineiventris* group, Deleninae) and a fragmented crab. These findings are in congruence with our observations of an arboreal-aquatic life habit in the Talaud monitor lizards.

Parasites: Some specimens exhibited several ticks (probably *Amblyomma* sp.) on the ventral side mostly near the umbilical region and at the base of the tail.

Reproduction: Mating behaviour was observed near the coast only two meters alongside a dirt road at 10.30 a. m., 19 July 2005. Two monitor lizards (MZB Lac. 5177 and MZB Lac. 5180) in mating position were discovered at a palm trunk about six meters above ground. When a local collector climbed up the coconut palm, the pair uncoupled and both specimens tried to hide in the crown. One of the specimens even jumped down the palm to escape. This behaviour was observed twice while chasing monitor lizards on Salibabu Island.

In addition, two voucher specimens (ZFMK 87587 and MZB Lac. 5177) contained two and three eggs, respectively, suggesting that the reproductive period of Talaud monitor lizards occurs throughout May, June and July at least. The two small eggs are ca. 8 x 17 mm in size, while the three well-developed eggs measure 29 x 63 mm, 28 x 63 mm, and 27 x 61 mm, respectively.

Taxonomy: De Rooij (1915), de Jong (1928) and Brandenburg (1983) referred the Talaud population to the Pacific monitor lizard, *V. indicus*. However, due to particular characteristics in color pattern and pholidosis together with molecular genetic evidence (Ziegler et al. 2007), the Talaud monitor lizards represent a new member of the *V. indicus* species group (Koch et al. subm.).

SERPENTES

Typhlopidae

***Typhlops* sp.**

***Material examined*:** MZB Serp. 3227 (AK045).

Distribution: First record of a blind snake species for the Talaud Islands.

Ecology: Two specimens were found under a coconut shell in a plantation near the coast of which one specimen was preserved.

Morphology & Taxonomy: ToL 130 mm; body width 2.2 mm; 255 ventrals, 13 or 14 subcaudals. The voucher specimen resembles the drawing of the holotype of *T. hedraeus* (CAS-SU 12346) depicted by in den Bosch & Ineich (1994) in having the eye restricted to the ocular scale not reaching the suture to the preocular; a subocular, in contrast to *T. ater* from Sulawesi, the Moluccas and New Guinea, is absent. However, the voucher differs from *T. hedraeus* in having two instead of one preocular and the latter is not smaller than the ocular. The upper jaw is not visible laterally. *T. hedraeus* is found on several Philippine Islands including Mindanao, Luzon and Negros, the type locality. Due to differences in morphology, the Talaud population may represent a distinct species.

Boidae

***Candoia paulsoni tasmai* Smith & Tepedelen in Smith et al. 2001** (Fig. 16)

***Material examined*:** MZB Serp. 2949, Niampak, Karakelong Island, 21 March 1999; MZB Serp. 2950, Essang, Karakelong Island, coll. WCS 5 April 1999.

***Additional material*:** MCZ 45767 (paratype), Karakelong, coll. Fairchild Garden Expedition 1940; ZMA 16937, Gunung Doeata (= Mt. Duata), Karakelong, coll. H. J. Lam 1926; ZMA 16943 (4 spec.), Liroeng (= Lirung), Salibabu, coll. M. Weber 1899

Distribution: Beside Talaud, *C. paulsoni tasmai* inhabits Halmahera and surrounding islands as well as the tip of North Sulawesi (Smith et al. 2001; de Lang & Vogel 2005). Consequently, the Talaud Islands are the most north-western population of this subspecies which is separated by about 800 km from the remaining subspecies of *C. paulsoni* on New Guinea and the Solomon Islands (Smith et al. 2001). In contrast, *C. carinata* is found on Sangihe Island enclosed between *C. paulsoni* on the Talaud Islands in the north and the northern peninsula of Sulawesi in the south. However, historical records of *Candoia* from the "Minahassa" peninsula, North Sulawesi, by Meyer (1887) and independently by Boettger (1898) as adopted by Boulenger (1897), de Rooij (1917), Sternfeld (1920), McDowell (1979), in den Bosch (1985), Iskandar & Nio (1996), Smith et al. (2001), and de Lang & Vogel (2005) may be incorrect as was repeatedly assumed for some others of Meyer's vertebrate collections (see Hickson [1889: 158] and Stresemann [1939: 305] for birds and Feiler [1990] for mammals, respectively). Confusion of locality data may have easily occurred since Meyer did not exclusively undertake his collection on the Minahassa peninsula of Sulawesi, but also purchased many voucher specimens from Charles W. Cursham, a trader in Manado, who in turn sent out native hunters (Meyer & Wiglesworth 1898). Intense fieldwork in North Sulawesi in recent years has revealed no voucher specimens confirming the historical records (J. McGuire pers. comm., Koch & Arida unpubl. data). It is, therefore, reasonable to suggest that the "Minahassa" specimen (not present in the MTD collection and most probably lost dur-

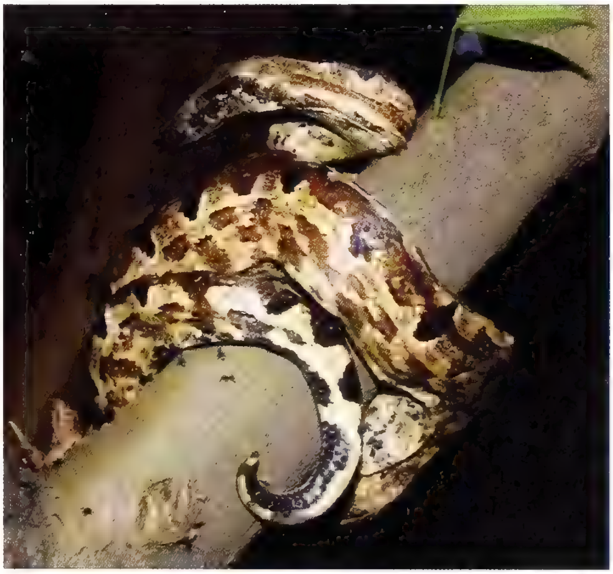

Fig. 16. *Candoia paulsoni tasmai* (MZB Serp. 2950) from Karakelong Island. Photo by André Koch.

ing World War II, U. FRITZ & E. LEHR pers. comm.) actually originated from Talaud or Halmahera with its satellite islands, the actual range of *C. paulsoni tasmai*. The same may apply to BOETTGER's (1898; 1903) specimen (collected by W. KÜKENTHAL, presumably in the Senckenberg Museum collection, Frankfurt), which also lacks exact locality data.

Morphology: Although we did not find this snake species during our survey, two specimens (see 'additional material') collected on Karakelong Island by a team of WCS lead by Jon RILEY, were examined in the MZB collection. These specimens (SVL 524/650 mm, TL 78/80 mm; TL/SVL+TL: 0.13/0.11) fit the definition by SMITH & TEPEDELEN in SMITH et al. (2001) in having 30/31–37/38–26/26 scales around the body (anterior–midbody–posterior), 179/183 ventrals, 36/36 subcaudals, only one enlarged supraocular reaching the orbit, 11/11 circumorbitals, 10/10 supralabials (6-7/5-7 contacting orbit), 10/13 infralabials, dorsals keeled except for the second to fifth lateral rows; a distinctive white postanal spot is missing. The color pattern of the specimens varies. Specimen MZB Serp. 2949 shows a reddish-brown background color with darker blotches indicating a faded zigzag band dorsally, the head becoming dark brown towards the tip; ventral side beige with brown mottling or blotches. In contrast, specimen MZB Serp. 2950 (Fig. 16), like the Talaud specimen examined by SMITH et al. (2001), has a relatively light beige background color with a distinctive dark red-brown zigzag band dorsally and indistinctive brown blotches laterally; markings of the tail are dark brown. The ventral side shows nearly the same coloration as the dorsal with darker mottling and blotches.

Taxonomy: Earlier authors (e.g., DE ROOIJ 1917, DE JONG 1928, DE HAAS 1950, MCDOWELL 1979) referred specimens from the Talaud Islands to *Candoia carinata* (formerly known as *Enygrus carinatus*), which was later split into three different species, i.e., *Candoia carinata*, *C. superciliosa*, and *C. paulsoni* with several subspecies (SMITH et al. 2001). Based on only one voucher specimen (MCZ 45767 from Karakelong), these authors allocated the Talaud population of bevelnosed boas to a new subspecies, *C. paulsoni tasmai*.

Pythonidae

Python reticulatus (Schneider, 1801)

***Material examined*:** none

Distribution: This widespread snake species inhabits continental South and Southeast Asia, the Philippines and Indonesia, east to the Moluccas and the Tanimbar Islands. The reticulated python was reported from Bitunuris on Salibabu Island (DE LANG & VOGEL 2005).

Ecology: From Salibabu Island it was reported that a python approximately 5 m long had killed a child (KOPSTEIN 1927, 1930). DE LANG & VOGEL (2005) recounted several cases of persons devoured by pythons. They extrapolated that every year at least one human is eaten in Sulawesi by a reticulated python.

Taxonomy: As was shown by AULIYA et al. (2002), even small island populations like those from Tanahjampea and Selayar, located between the south-western peninsula of Sulawesi and Flores in the Lesser Sunda Islands, show subspecific differentiations. The Sangihe Island population also represents a distinct lineage (AULIYA et al. 2002). Therefore, the systematic status of the Talaud population compared to those of the Philippines, Sulawesi and the Moluccas is unclear and deserves taxonomic revision.

Colubridae

Remarks: One medium-sized brown snake disappeared under stones when encountered in a narrow gorge with a small stream (Fig. 4). Another small brown snake was encountered near the root of a tree, indicating that, apart from the following species, further unknown snakes inhabit the Talaud Islands.

Boiga irregularis (Bechstein, 1802)

***Material examined*:** MZB Serp. 3238 (AK048).

Distribution & Ecology: The brown tree snake *Boiga irregularis* is a widespread species known from most islands east of Sulawesi, and reaching Australia. In some Pacific islands where *B. irregularis* was accidentally introduced, it has been responsible for a dramatic decline in the native vertebrate faunas (e.g., RODDA & FRITTS 1992; RODDA et al. 1997). One road kill was found in the vicinity of Lirung, Salibabu Island. This is the first record of *B. irregularis* for the Talaud Archipelago.

Morphology: One preocular, two postoculars, one loreal; eight supralabials, the fourth to sixth in contact with orbit; ten and eleven infralabials, respectively; 19 scales around body, about 247 ventrals and 115 subcaudals; the vertebrals are slightly enlarged. The specimen shows a narrow pattern of indistinct light and dark grey cross-bands particularly on the anterior half of body as is typical for some *B. irregularis*.

Cerberus r. rynchops (Schneider, 1799)

***Material examined*:** none

***Additional material*:** RMNH 6262, Karakelong, coll. Dr. H. Boschma 14–21 June 1930.

Distribution: This widespread homalopsine snake is known to occur from continental Southeast Asia through the Philippines and Indonesia reaching New Guinea (Gyi 1970; Alfaro et al. 2004). De Jong (1928) reported the species for Karakelong as did Brongersma (1934) based on a specimen (see 'additional material') collected in 1930. While de Haas (1950) listed only the Talaud Islands in the species account of *C. rynchops*, Salebabu (= Salibabu) Island is mentioned in the distribution appendix.

Taxonomy: Gyi (1970) recognized two subspecies: the widely distributed *C. r. rynchops* and *C. r. novaeguineae* from New Guinea. According to de Lang & Vogel (2005) the Talaud population belongs to the nominotypic subspecies. Alfaro et al. (2004), however, demonstrated that *C. r. rynchops* is split into four to five phylogenetic lineages (India and Myanmar, Philippines, Greater Sunda Islands and Sulawesi, and the Thai-Malay Peninsula and Gulf of Thailand). Thus, the taxonomic status of the Talaud population remains unclear.

CROCODYLIA

Crocodylidae

Crocodylus sp.

***Material examined*:** none

Taxonomy: In 1997 two unidentified crocodiles were observed on Karakelong Island (J. Riley, pers. comm. in Platt & Lee 2000). Although currently the taxonomic status of the Sulawesi populations and hence that of the Talaud Archipelago is still unsolved, it is reasonable to suggest that the widespread *Crocodylus porosus* or another species, *C. mindorensis* from the Philippines, respectively, inhabits the Talaud island group (Platt & Lee 2000; Platt et al. 2007).

Ecology: Reportedly, these crocodiles live in mangrove swamps which are threatened by destruction. However, apparently due to religious taboos villagers do not kill crocodiles (J. Wardill, pers. comm. in Platt & Lee 2000).

TESTUDINES

Cheloniidae

Chelonia mydas (Linnaeus, 1758)

***Material examined*:** none

Ecology: *Chelonia mydas* is known to have nesting sites on the Talaud Islands (Whitten et al. 2002). Although no trade with sea turtles and their products was noticed on Salibabu Island, repeated observations were made in the markets of Manado and elsewhere on North Sulawesi that sea turtles and their eggs were sold for human consumption.

4. DISCUSSION

Species diversity, island endemicity and nature conservation

Some authors have pointed out the depauperate but highly endemic character of the nearby Sangihe and Talaud Archipelagos (e.g., Lazell 1992; Riley 2002). This statement partly contradicts the geological assumption that the Talaud block did not emerge above sea level until the Pleistocene (Moore et al. 1981). Repeated drops in global sea levels during the Pleistocene did probably not connect the Talaud Archipelago with the neighboring Sangihe Islands, from which it is separated by a deep ocean trench, or with any other surrounding landmasses (Voris 2000). Accordingly, Lazell (1992) hypothesized that amphibians and reptiles must have colonized Talaud by overwater dispersal. Faunal and floral colonizers of the Talaud Archipelago had presumably less than two million years to succeed or even to evolve endemic lineages. Thus, the degree of endemism of Talaud's herpetofauna is relatively low (only 4 %). Currently, only *Varanus* sp. seems to be restricted to the island group but the number of Talaud endemics may increase by up to 27 % in the future, when the taxonomic status of some problematic specimens belonging to widespread species or species groups has been clarified (e.g., *Nactus* cf. *pelagicus*, *Cyrtodactylus* cf. *jellesmae*, *Hydrosaurus* sp., *Lamprolepis smaragdina* ssp., *Callulops* cf. *dubius*, and *Typhlops* sp.). Detailed systematic investigations including modern molecular techniques are needed to solve their taxonomic identity.

As expected for small oceanic islands (Sternfeld 1920; Brown 1957; Adler et al. 1995; Allison 1996; Crombie & Pregill 1999), skinks (next to geckos) are the most diverse reptile group on the Talaud Islands, while amphibians are very rare due to their limited ability to cross saltwater barriers. However, no *Sphenomorphus* skinks were found during our biodiversity survey on Salibabu Island although this taxonomically difficult and diverse genus is well represented on the adjacent islands of Sulawesi, Halmahera and Mindanao (Brown & Alcala 1980; Iskandar & Nio 1996; Monk et al. 1997). In addition, flying lizards of the genus *Draco* were not observed during our field work, nor during previous expeditions to Salibabu Island (de Jong 1928; McGuire et al. 2007). In contrast, Lazell (1992) predicted the sympatric occurrence of two *Draco* species for Talaud, one of which he assumed to be a giant, based on biogeographic knowledge of the Lesser Antilles *Anolis* lizards. Therefore, future field surveys concentrating on the forested areas of the larger island of Karakelong are needed to verify the presence of *Draco* spp. on the Talaud Islands. The same applies to *Gekko vittatus* and *Bronchocela jubata*, which have been reported from Talaud in the past (see above). Further unrecognized amphibian and reptile species may be anticipated to inhabit the Talaud Archipelago.

As in many Pacific island biotas and beyond, *Boiga irregularis*, *Gehyra mutilata*, and *Hemidactylus frenatus* are most probably non-native, naturalized species of the Talaud Archipelago. Because these reptiles are not utilized by man, they have likely reached this island group via accidental human-mediated transportation. Nevertheless, the ability to "use" boats and ferries for over-water dispersal renders these three species as candidates to cross far distances on natural rafts as well. A determination between accidental human-mediated displacement on the one hand and natural colonization on the other seems virtually impossible.

In any case, the new record of the invasive brown tree snake *B. irregularis* for Talaud may have severe consequences for the native vertebrate fauna of this island group. As was demonstrated by several studies (e.g., Savidge 1987; Rodda & Fritts 1992; Rodda et al. 1997), this snake species is responsible for the dramatic decline in bird and lizard populations on Guam. This could be particularly fatal for endemic lizard species like the Talaud monitor lizards which have a very restricted distribution range (Koch et al. subm.). Savidge 1988 and McCoid et al. (1994) reported from Guam that *B. irregularis* even preys on juveniles of *Varanus indicus*. Therefore, the development of the Talaud population of this invasive snake species deserves special attention in the future.

Deforestation and destruction of natural habitats represent another major threat to the amphibians and reptiles of the Talaud Archipelago as was pointed out by Riley (2002) for the mammals of this island group. Coconut plantations replace natural vegetation in most areas. Therefore, a wildlife reserve has been established on the larger island of Karakelong to protect endemic faunas (Riley 1997).

Biogeographic relations and past dispersal routes

Although it may seem premature, some conclusions can be drawn about the biogeographic origin and affinities of the Talaud Islands' herpetofauna based on current distribution patterns of amphibians and reptiles of the Indo-Australian Archipelago. Firstly, several typical Australopapuan species or species groups (viz. *Litoria infrafrenata*, *Candoia paulsoni*, *Nactus* cf. *pelagicus*, *Eugongylus rufescens*, *Lipinia noctua*, and *Varanus* sp. [aff. *indicus*]), reach their most north-western distributions on the Talaud Islands. These Australopapuan faunal elements probably arrived at this island group via Halmahera and adjacent islands in the northern Moluccas. Some species with Oriental origin, such as *Eutropis multifasciata* and *Eutropis* cf. *rudis*, have their most easterly distribution on or around the Talaud Islands. Consequently, the Talaud Archipelago's biogeographic position within the Wallacea transition zone is clearly warranted (see Cox 2001 for a recent review of the Wallacea region). Interestingly, few widespread Oriental species like *Varanus salvator* did not reach the Talaud Archipelago despite its abundance on Sulawesi and smaller off-shore islands. An explanation for this may be the flow of Pacific water into the Indian Ocean via the Indonesian seas. This throughflow enters the Indonesian Islands in north-eastern to south-western direction between Mindanao and the Talaud group passing the Celebes Sea while another sea current from the Pacific circulates between Talaud and Halmahera (Gordon & Fine 1996, Gordon 2005), thus hampering over-water dispersal on natural rafts.

Secondly, the herpetofauna of Talaud shows clear biogeographic relations to Halmahera in the northern Moluccas and, to a lesser extent, to Sulawesi and to the Philippines. With the northern Moluccas the Talaud Archipelago has 20 amphibian and non-marine reptile species in common, while it shares only 14 amphibians and non-marine reptiles with Sulawesi and the Philippines, respectively (see Tab. 1). With regard to amphibians, two out of three Talaud species also occur on Halmahera and, at least in one case (*Litoria infrafrenata*), farther southeast on New Guinea and adjacent islands. In contrast, no frog species from the Philippines seem to have reached the Talaud Islands. *Limnonectes modestus* which inhabits Sulawesi is also found on the Talaud Islands and some islands of the Moluccas. For the terrestrial reptiles, four species (respectively five when *Gekko vitattus* is included) are exclusively shared by the Talaud Archipelago and the northern Moluccas including areas further southeast. These are *Candoia paulsoni tasmai*, *Nactus* cf. *pelagicus*, *Eugongylus rufescens*, and *Lipinia noctua*.

Due to their central position in the Molucca Sea, there are no native species exclusively common to the Talaud Is-

Table 1. Distribution records of amphibians and reptiles from the Talaud Islands as compared to the surrounding islands of Sulawesi, Halmahera and the Philippines. Probable non-native, i.e. invasive species of the Talaud Islands are indicated by a hash key (#). New records for the Talaud Island are marked with an exclamation mark (!); new records for Salibabu Island are denoted by an asterisk (*). An "(x)" denotes that different subspecies or closely related taxa of a species complex, respectively, are involved. [1] indicates that Nactus cf. pelagicus has only been recorded from Morotai but due to close proximity most probably also occurs on Halmahera. Locality records for surrounding islands are taken from Boettger (1895a, b; 1903), Boulenger (1897), Barbour (1912), de Rooij (1915; 1917), de Jong (1928), Tanner (1950), Brown & Alcala (1970), Brown & Alcala (1980), Brown (1991), Monk et al. (1997), Hallermann (2005), and Ziegler et al. (2007).

	Locality			
Taxon	**Sulawesi**	**Talaud**	**Halmahera**	**Philippines**
ANURA				
Hylidae (1 sp.)				
Litoria infrafrenata		x	x	
Microhylidae (1 sp.)				
Callulops cf. *dubius*		x!	x	
Ranidae (1 sp.)				
Limnonectes cf. *modestus*	x	x	(x)	(x)
SAURIA				
Agamidae (3 spp.)				
Bronchocela cristatella	x	x	x	x
Bronchocela jubata	x	?		?
Hydrosaurus sp.	(x)	x*	(x)	(x)
Gekkonidae (5 spp.)				
Cyrtodactylus cf. *jellesmae*	x	x*	(x)	
Gehyra mutilata #	x	x!	x	x
Gekko vitattus		?	x	
Hemidactylus frenatus #	x	x	x	x
Nactus cf. *pelagicus*		x!	x[1]	
Scincidae (8 spp.)				
Emoia a. atrocostata	x	x*	x	x
Emoia caeruleocauda	x	x	x	x
Eugongylus rufescens		x	x	
Eutropis m. multicarinata		x*		x
Eutropis multifasciata	x	x!	x	x
Eutropis cf. *rudis*	x	x!		x
Lamprolepis smaragdina ssp.	(x)	x	(x)	(x)
Lipinia noctua		x	x	
Varanidae (1 sp.)				
Varanus sp. (aff. *indicus*)		x	(x)	
SERPENTES				
Typhlopidae (1 sp.)				
Typhlops sp.		x!		(x)
Boidae (1 sp.)				
Candoia paulsoni tasmai	?	x	x	
Pythonidae (1 sp.)				
Python reticulatus	x	x	x	x
Colubridae (2 spp.)				
Boiga irregularis #	x	x!	x	?
Cerberus r. rynchops	x	x	x	x
CROCODYLIA				
Crocodylidae (1 sp.)				
Crocodylus sp.	x	x	x	x
TESTUDINES				
Cheloniidae (1 sp.)				
Chelonia mydas	x	x	x	x

lands and the Philippines and Halmahera, and only one species, *Eutropis* cf. *rudis*, in common with the Philippines and Sulawesi. However, some widespread non-invasive species like *Cerberus rynchops*, *Python reticulatus*, *Bronchocela cristatella*, *Emoia atrocostata*, *E. caeruleocauda*, *Eutropis multifasciata*, and *Lamprolepis smaragdina* are found at all four localities. It seems plausible that such widespread species were exchanged between the Philippines and the Moluccas by using Sulawesi as a stopover rather than the Talaud Islands (but see below). Hence, the Philippines may have been colonized via the Sangihe Island chain or arrived at the Moluccas via the Banggai-Sula Islands finally reaching the Talaud Archipelago in the north. Nevertheless, it remains doubtful whether the Talaud Islands served as natural stepping stones (particularly during periods of lowered Pleistocene sea levels) on the dispersal route between the Philippines and North Sulawesi. Inger (1954) argued that the present distribution of the genus *Oreophryne* Boettger, 1895, which also occurs on Sulawesi and some islands of the Lesser Sundas may account in favor of the Moluccan-Talaud corridor. *Oreophryne*, however, was never recorded from the Talaud Islands. The same applies to the genus *Cornufer* Tschudi, 1838 (currently a synonym of *Platymantis* Günther, 1858), which ranges from the Philippines through the Moluccas to New Guinea and the Solomons, but is not known from Sulawesi. According to Inger (1954), this taxon constitutes more evidence for the Talaud avenue between the Philippines and the Moluccas which also was later identified as major route of faunal dispersal by Holloway & Jardine (1968). In either case, the extinction or replacement of former Talaud populations by later invaders may explain their absence from the island group. As noted by Whitten et al. (1987) biological evidence for a stepping stone hypothesis between the Philippines and the Moluccas via Talaud is still insubstantial. Only further field work and detailed morphological comparisons of sufficient material together with molecular investigations including individuals from all areas involved could trace the unique history for each single species and the region.

Comparison with other organism groups

Distribution patterns of some other organism groups vary from the herpetological results presented here. Vane-Wright & de Jong (2003) traditionally included the Talaud Islands as part of the Sulawesi region in their review of Sulawesi butterflies. They predicted that colonization from the Philippines into North Sulawesi happened via Sangihe and Talaud. Likewise, Natus (2005) in her analysis of endemic centers of Indonesian vertebrates defined the Sulawesi region as the mainland of Sulawesi plus surrounding island groups like Sangihe and Talaud in the north. Interestingly, our herpetological results contradict the findings in butterflies by Vane-Wright & de Jong (2003) who eventually concluded that the fauna of the Talaud Archipelago most probably "belongs" to the Mindanao fauna.

With regard to mammals, the Talaud and Sangihe Islands are home to an endemic marsupial, the Talaud bear cuscus (*Ailurops ursinus melanotus*). These populations represent the northernmost subspecies of this Sulawesian phalanger (Feiler 1977; 1990). At the same time, *A. ursinus* is the only example of a non-volant and non-invasive mammal that inhabits both neighboring archipelagos (Riley 2002). Human translocation could be responsible for the exceptional distribution pattern of this species which is frequently hunted as food. On the other hand, both island groups harbor their own endemics, e.g., *Tarsius sangirensis* on Sangihe and *Melomys caurinus* on Talaud (Riley 2002), which have their respective closest relatives on North Sulawesi and the northern Moluccas (Flannery 1995; Menzies 1996; Shekelle 2003). There is another population of *T. sangirensis* on the nearby Siau Island, which may warrant a separate taxonomic status (Brandon-Jones et al. 2004). As a result, these mammal taxa confirm the minor faunal similarity between Sangihe and Talaud, and at the same time, supply evidence for their close biogeographic relationships with Sulawesi and New Guinea, respectively.

Consequently, the tradition to incorporate the Talaud Archipelago into the Sulawesi subregion within the transitional zone of Wallacea seems only conditionally justified from a herpetofaunistic point of view. Rather, this island group should be recognized as part of the northern Moluccan subregion with closer zoogeographical links to Halmahera compared with Sulawesi or the Philippines. The transitional character of the herpetofauna of the Talaud Islands composed of both typical Oriental and Australopapuan faunal elements clearly reinforces the justification of the Wallacea region between Southeast Asian and Australopapuan biotas.

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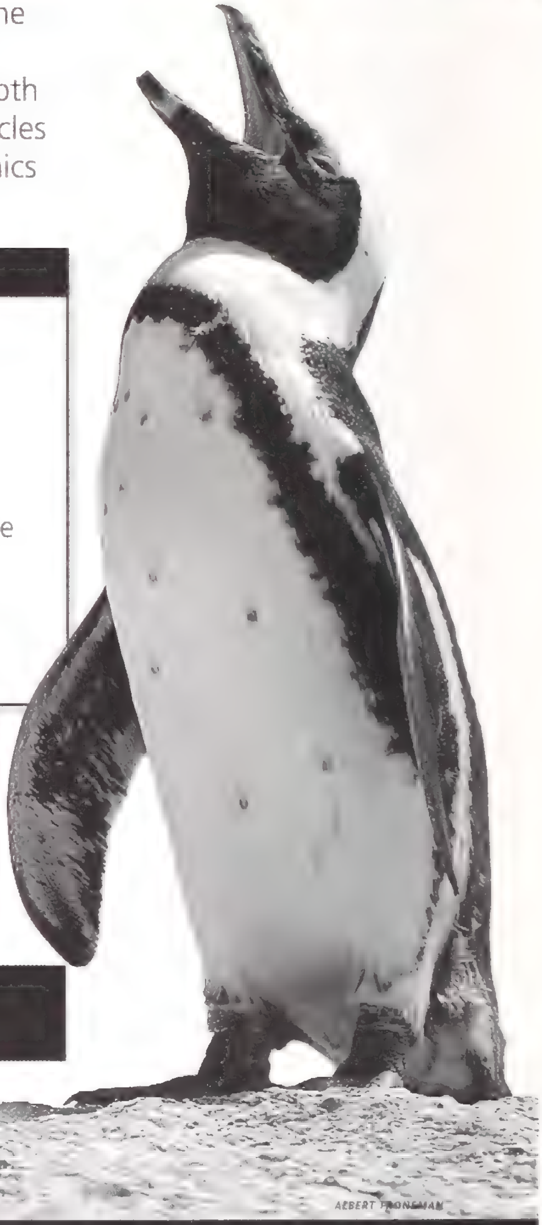

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Editorial

New species and records of mammals from Africa

Tropical Africa and surrounding islands such as Madagascar, the Comoros, Bioko, São Tomé and others are hotspots of vertebrate diversity. Although mammals have been the subject of research for centuries, the full diversity of African mammals is still not known, as new discoveries are being made every year (Reeder et al. 2007). From 1988 to 2008, 175 new taxa of mammals, including five new genera, 136 species, and 31 new subspecies, were named from this region (Hoffmann et al. 2009). Primates, rodents, bats and shrews are the mammal groups in which most new discoveries were made. These discoveries add to the common knowledge of the world's biotic richness, but they also have strong implications for conservation measures (Ceballos & Ehrlich 2009). Yet, it is an alarming fact that very little is known about the biology and full distributional range of most of these newly discovered taxa. The reviews of Reeder et al. (2007) and Hoffmann et al. (2009) show that the discovery of new mammals in Africa is continuing. In 2009, three species of bats and two species of shrews from Africa have been named so far: *Miniopterus aelleni* (Goodman et al. 2009; Madagascar), *Mops brachypterus* (Stanley et al. 2009; Pemba Island), *Triaenops menamena* (Goodman & Ranivo 2009; Madagascar), *Suncus hututsi* (Kerbis Peterhans & Hutterer 2009; Burundi), and *Sylvisorex akaibei* (Mukinzi et al. 2009; D. R. Congo).

The present issue includes five papers which describe new species of mammals from Africa, two rodents and three shrews. Another paper presents new distributional data of small mammals from Mount Kupe in Cameroon, including a new record of the recently described *Hylomyscus walterverheyeni.* It continues the tradition of the Zoologisches Forschungsmuseum Alexander Koenig in taxonomic research on African mammals, mainly associated with the name of its former director Martin Eisentraut, and of Bonner zoologische Beiträge publishing pertinent studies (e.g. Hutterer 1992).

This issue is also a tribute to four scientists, three still active and one deceased, who have served the scientific community highly, three of them for a very long time.

Michael D. Carleton, curator of mammals at the National Museum of Natural History, Smithsonian Institution, Washington, D.C., is honoured by associating his name with a new species of *Eliurus* from Madagascar (Goodman et al., this issue). Carleton has revised various groups of rodents from Africa and Madagascar, and is well known for his monumental work, together with Guy G. Musser, on the rodents of the world (Carleton & Musser 2005).

Duane A. Schlitter, former curator of mammals at the Carnegie Museum of Natural History, Pittsburg, is honoured by associating his name with a remarkable new species of *Surdisorex* from Kenya, the third species of the genus (Kerbis Peterhans et al., this issue). Schlitter has promoted the scientific study of mammals in various African countries such as Kenya, Somalia, Namibia, and South Africa, and served the scientific community by organizing and supporting several successful meetings on "Ecology and Taxonomy of African Small Mammals" (Schlitter 1978).

Gordon B. Corbet, former curator of mammals at The Natural History Museum, London, is honoured by associating his name with the largest species of *Sylvisorex* ever discovered. He has served the scientific community by writing a number of textbooks on the mammals of the Palaearctic Region, Indomalayan Region, and the World (e.g. Corbet & Hill 1991), and by revising African mammals such as hedgehogs, hyraxes, and hippos.

Hans G. Rupp, who is honoured by associating his name with a new species of *Dendromus* from Sudan (Dieterlen, this issue), was a German student of zoology based at the University of Tuebingen. He was an excellent field biologist and studied the ecology and distribution of rodents in Sudan and Ethiopia (Rupp 1980), often together with Gerhard Nikolaus, and both discovered numerous new species of mammals, including the one now named for Rupp. He died in Kenya in 1979, at the age of 32.

We are grateful to all these colleagues for their great service, and also to the authors of this issue for their participation in this project.

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A new species of *Eliurus* Milne Edwards, 1885 (Rodentia: Nesomyinae) from the Réserve Spéciale d'Ankarana, northern Madagascar

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Abstract. The nesomyine rodent *Eliurus antsingy* is presently known from disjunct limestone regions in the dry lowland forests of northern and western Madagascar. Previous studies of *E. antsingy* noted morphological variation among isolated populations but recognized only a single species. Herein, we examine morphological and genetic variation within and among populations of *E. antsingy* with a particular focus on the taxonomic status of a population from the Réserve Spéciale d'Ankarana in the extreme north of the island. Whereas morphometric analysis cannot distinguish the Ankarana population from its nearest neighbor ~500 km to the south (Namoroka), both are morphologically distinguishable from a population of *E. antsingy* from the type locality (Bemaraha). In contrast, genetic data reveal substantial interpopulation divergence among all three populations, and phylogenetic analysis of these data indicates that the two morphologically similar forms do not form a clade. Based on these results we recognize the population from the Réserve Spéciale d'Ankarana as a new species but given the limitations of current sampling, retain the other two populations as *E. antsingy*.

Keywords. *Eliurus*, Nesomyinae, Rodentia, new species, Ankarana, Madagascar.

1. INTRODUCTION

Of the nine genera of living rodents native to Madagascar (Rodentia: Nesomyidae: Nesomyinae), the genus *Eliurus* Milne Edwards, 1885 is by far the most species-rich. As currently understood, the genus comprises 11 species, five of which have been described since 1994 (MUSSER & CARLETON 2005; CARLETON & GOODMAN 2007). Whereas most of these taxa are known from Madagascar's humid eastern and central forest biomes, two occur in lowland dry forests of the island's western regions. Of these, *E. myoxinus* Milne Edwards, 1885 is a relatively small-bodied form that is broadly distributed throughout western dry forests and into some humid forest areas of the northeast (SOARIMALALA & GOODMAN 2003). The second, larger species, *E. antsingy* Carleton, Goodman & Rakotondravony, 2001 has a disjunct distribution and, with the exception of one site, is presently known only from forested habitats that occur on heavily eroded limestone outcroppings known as *tsingy* (Fig. 1). Two specimens of *E. antsingy* were collected in 1964 in the Parc National (PN) de Bemaraha and comprise the holotype and one paratype of this taxon (CARLETON et al. 2001). In this same publication, four additional specimens collected from the Réserve Naturelle Intégrale (RNI) de Namoroka in 1999 were also provisionally referred to *E. antsingy*. However, in the course of the description of this taxon, the authors noted that "existing sample sizes of *E. antsingy* are smaller than desirable" and urged "the need for continued study to clarify the interpopulational variation noted" (CARLETON et al. 2001, p. 979).

In the time since the original species description of *E. antsingy* was published, additional specimens of a relatively large *Eliurus* were collected from *tsingy* habitats at Ankarana and a nearby zone of metamorphic rock outcrops near Daraina (Fig. 1); these animals were all provisionally assigned to *E. antsingy* (CARLETON & GOODMAN 2007). With the addition of these new records, these authors noted that the "overall amount of craniodental differentiation among the three regions [Bemaraha, Namoroka, and the northern Ankarana + Daraina region] approximates that derived among samples of the broadly distributed *E. majori* [Thomas, 1895]… and they marginally overlap in morphometric space" (CARLETON & GOODMAN 2007, p. 15). This morphometric variation in animals referred to *E. antsingy*, coupled with the disjunct distribution of this species, suggest that these isolated populations might be genetically distinct as well. However, to date no molecular data have been brought to bear on intraspecific differences within this species group. Herein, we examine variation within *E. antsingy* using a combination of morphometric and molecular data, with a particular focus on the taxonomic status of the northern populations from Ankarana.

2. MATERIALS AND METHODS

Taxon sampling. Specimens employed in this study are from the following museums: Field Museum of Natural History, Chicago (FMNH); Muséum national d'Histoire naturelle, Paris (MNHN); and Département de Biologie Animale, Université d'Antananarivo, Antananarivo (UADBA). Coordinates used to compose the range map are those given by collectors (see Appendix 1) or those estimated by CARLETON et al. (2001).

For our morphometric analyses, we compare specimens from four localities (Fig. 1; see Appendix 1 for specific information on specimens):

A. *Eliurus antsingy* group (CARLETON & GOODMAN 2007)
  1. *Eliurus antsingy* from the Bemaraha formation (FMNH, MNHN, n=3)
  2. *Eliurus antsingy* from the Namoroka formation (FMNH, UADBA, n=14)
  3. *Eliurus antsingy* from the Ankarana formation (FMNH, n=9)

B. *Eliurus majori* group (CARLETON & GOODMAN 2007)
  1. *Eliurus majori* Thomas, 1895, from the montane forests of Montagne d'Ambre (FMNH, n=20). *Eliurus majori* has a broad distribution across the island in montane forest, but the population from Montagne d'Ambre is notably smaller than most other populations of this species. On the basis of body size and geographic proximity, the Montagne d'Ambre population of *E. majori* is the closest to the *E. antsingy* from Ankarana and was therefore included here for comparison.

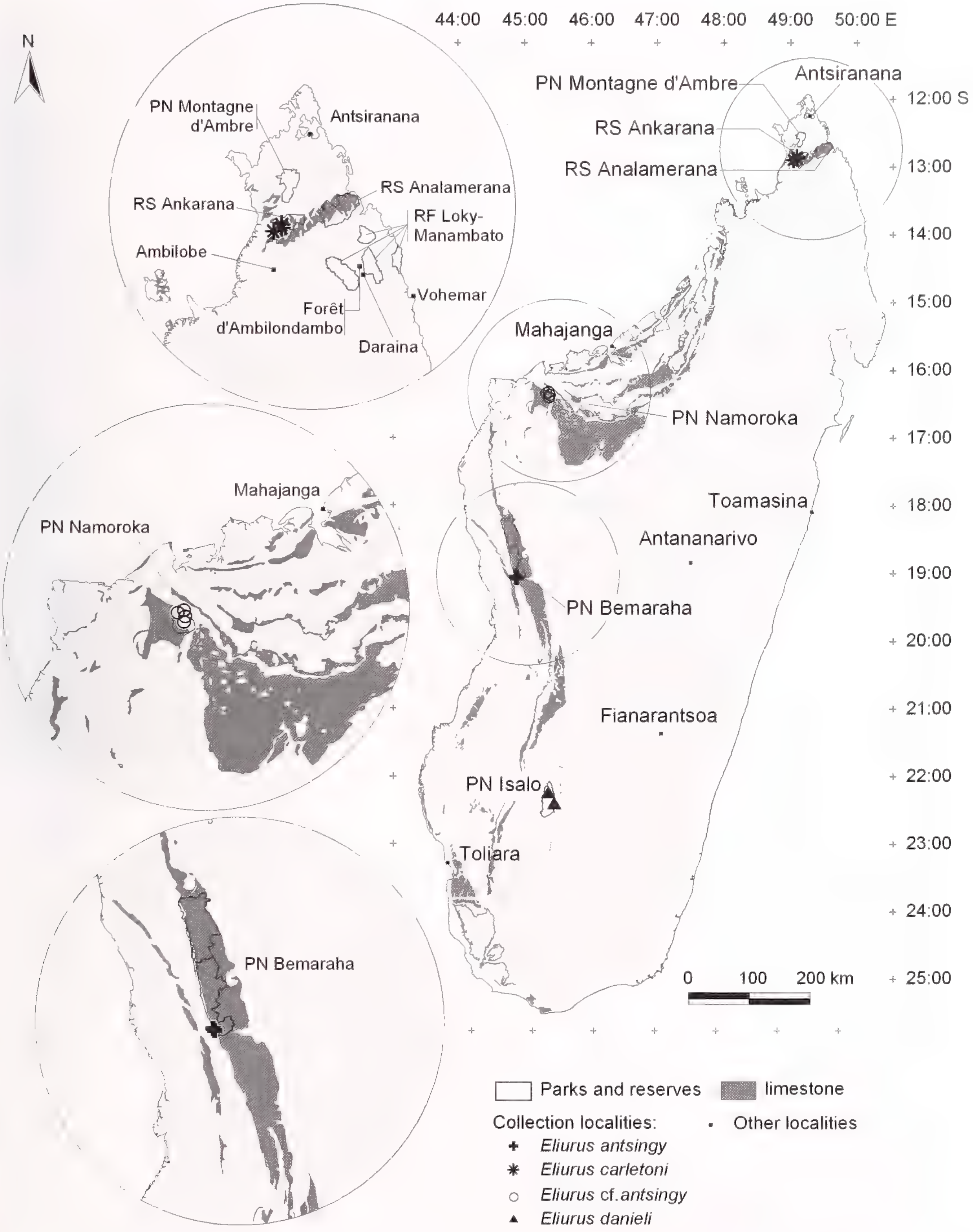
Morphometric comparisons. We included six external (including mass in g) and 18 craniodental measurements for each specimen. External measurements were obtained from the collectors' original field catalogs or specimen labels and include the following: total length of body and tail (TOTL); head and body length (HBL); length of tail vertebrae (TL); hindfoot length (HFL, excluding claw length except as noted); ear length (EL); and weight (WT). Most of the external measurements were made by the same collector (Goodman).

The 18 craniodental variables (all measured by Goodman) were recorded to 0.1 mm using digital calipers and were based on the measurements defined by CARLETON (1994) and include the following: breadth of the braincase (BBC); breadth across both incisive foramina (BIF); breadth of the bony palate across the first upper molars (BM1s); breadth across the occipital condyles (BOC); breadth of the rostrum (BR); breadth of the zygomatic plate (BZP); depth of the auditory bullae (DAB); interorbital breadth (IOB); length of bony palate (LBP); length of diastema (LD); length of incisive foramen (LIF); coronal length of maxillary toothrow (LM1-3); length of rostrum (LR); occipitonasal length (ONL); posterior breadth of the bony palate (PPB); postpalatal length (PPL); width of the first upper molar (WM1); and zygomatic breadth (ZB). We have used GREENE (1963), VOSS (1988), and CARLETON (1994) for the morphological terms and landmarks used herein for craniodental characters.

We sorted all specimens into age categories using qualitative evaluation of tooth wear and the extent of cranial-suture fusion. Specimens with complete but unworn molar rows and an unfused basisphenoid suture were classed as young adults; those with slightly worn molar teeth and a fused basisphenoid suture were considered adults. External measurements from adults were used to establish general size differences between different *Eliurus* populations. Only adult specimens were used in craniodental statistical analyses, which included univariate and multivariate comparisons employing Statistica (version 7.1, series 0306) programs. The latter comparisons included principal component analyses using ln-transformed data and a correlation matrix.

Molecular data. DNA was extracted from 13 animals representing the three populations of *E. antsingy* described above using a DNeasy extraction kit (Qiagen Inc.). The entire cytochrome *b* (cyt-*b*) gene was amplified from genomic DNA using primers MVZ05 and UMMZ04 (see JANSA et al. 1999 for primer sequences). To generate fragments of a suitable size for sequencing, this PCR product was used as a template in two subsequent reamplification reactions, one using primer MVZ05 paired with UMMZ12 and one using UMMZ13 paired with UMMZ04. All PCR reactions were performed using reaction conditions as described in JANSA et al. (2006). All fragments were sequenced in both directions, and resulting sequences have been deposited in GenBank (accession numbers GQ420656-GQ420668).

The resulting cyt-*b* sequences were aligned by eye with reference to translated amino acid sequences. We included additional sequences from *E. majori* from northern (Montagne d'Ambre; FMNH 154610, Genbank Accession AF160552) and southern Madagascar (Midongy-Sud; FMNH 178686, GQ420668), as well as a specimen of *E. danieli* Carleton & Goodman, 2007 (UADBA 10483, AF160553) as outgroups. Phylogenetic analyses were performed using both maximum parsimony (MP) and maximum likelihood (ML) as implemented in PAUP*ver4.0b10 (SWOFFORD 2002). Tree searches using MP were performed using the branch-and-bound algo-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PN Montagne d'Ambre
Antsiranana
RS Ankarana
RS Analamerana
RF Loky-Manambato
Ambilobe
Vohemar
Forêt d'Ambilondambo
Daraina
Mahajanga
PN Namoroka
Toamasina
Antananarivo
PN Bemaraha
Fianarantsoa
PN Isalo
Toliara
0
100
200 km
Parks and reserves
limestone
Collection localities:
Other localities
Eliurus antsingy
Eliurus carletoni
Eliurus cf. antsingy
Eliurus danieli

Fig. 1. Map of Madagascar showing localities mentioned in the text. The complete map of the island to the right shows the island wide delineation of limestone deposits based on Bésairie's (1964) classification of the geology of Madagascar. These are extracted from his categories 14 and 18 "Marnes & calcaires" [=marls and chalks]. The three circular areas delineated on the full map are presented in finer detail in the left hand circular insets and in which the distribution of different *Eliurus* spp. are given.

rithm. For ML analyses, we first identified the best-fit model of nucleotide substitution using the Akaike information criterion (AIC) as employed in ModelTest ver. 3.6 (POSADA & CRANDALL 1998). We subsequently evaluated whether a molecular clock fit our data using a hierarchical log-likelihood ratio test. Parameters for the resulting best-fit model were fixed in a heuristic search using 10 replicates of random taxon addition and TBR branch swapping. Nodal support was calculated for both MP and ML analyses using non-parametric bootstrapping (FELSENSTEIN 1985). All bootstrap analyses employed 1000 pseudoreplicates analyzed with heuristic searches as above. Polymorphism and divergence statistics were calculated using DNAsp ver. 4.10 (ROZAS et al. 2003); in addition, we report ML-corrected divergence values as calculated in PAUP*.

3. RESULTS

After comparisons of the specimens from the Réserve Spéciale (RS) d'Ankarana, previously identified as *Eliurus antsingy*, using external and craniodental measurements and characters, as well as a molecular analysis, these animals represent a previously unknown species of Malagasy rodent falling within the *E. antsingy* group (sensu CARLETON & GOODMAN 2007). This new taxon is described below.

Superfamily Muroidea Illiger, 1811
Family Nesomyidae Major, 1897
Subfamily Nesomyinae Major, 1897

Eliurus carletoni, new species
Figs. 2–3; Tables 1–3

Holotype. An adult female specimen in the Field Museum of Natural History (FMNH 173105) prepared as skin, skull, and partial skeleton, collected 9 April 2002 by Steven M. Goodman (original number SMG 12832). The round skin and skull are in fine condition. Recorded external data include: TOTL, 335 mm; HBL, 143 mm; TL, 183 mm; HFL, 29 mm; EL, 25 mm; and WT, 99 gm. The basisphenoid suture is fused and third molar slightly worn. The animal was noted as having large mammae, no embryos or placental scars. The mammae formula was one axial pair and one inguinal pair. Muscle tissue samples were preserved in lysis buffer.

Type locality. Madagascar, Province d'Antsiranana, Réserve Spéciale d'Ankarana, Campement des Anglais (Anilotra), 7.5 km NW Mahamasina, 12°54.4'S, 49°06.6'E; 125 m above sea-level (Fig. 1).

Diagnosis. A species of *Eliurus* falling within the *E. antsingy* species group (sensu CARLETON & GOODMAN 2007) characterized by a dark brown dorsal pelage, contrasting grayish-white venter, unicolor dark brown tail (including terminal tuft), and short hind foot (HFL 28–29 mm) and ears (EL 23–25 mm) (Fig. 2). Cranial size moderately large (ONL 40–41 mm), rostrum relatively short for the genus (LR/ONL ca. 31%), molar rows moderately long (LM1-3 5.4–5.7 mm), incisive foramina notably short and wide (LIF/LD ca. 47–49%), palatine process short and stout, and auditory bullae relatively small in comparison to other members of the *E. antsingy* species group. Given present taxon and character sampling, the species is further diagnosed by the following 18 unreversed synapomorphies in the cyt-*b* gene (the first nucleotide given is the ancestral state, followed by the nucleotide position in the cyt-*b* gene, followed by the derived state. Changes that result in an amino acid replacement are shown in bold;

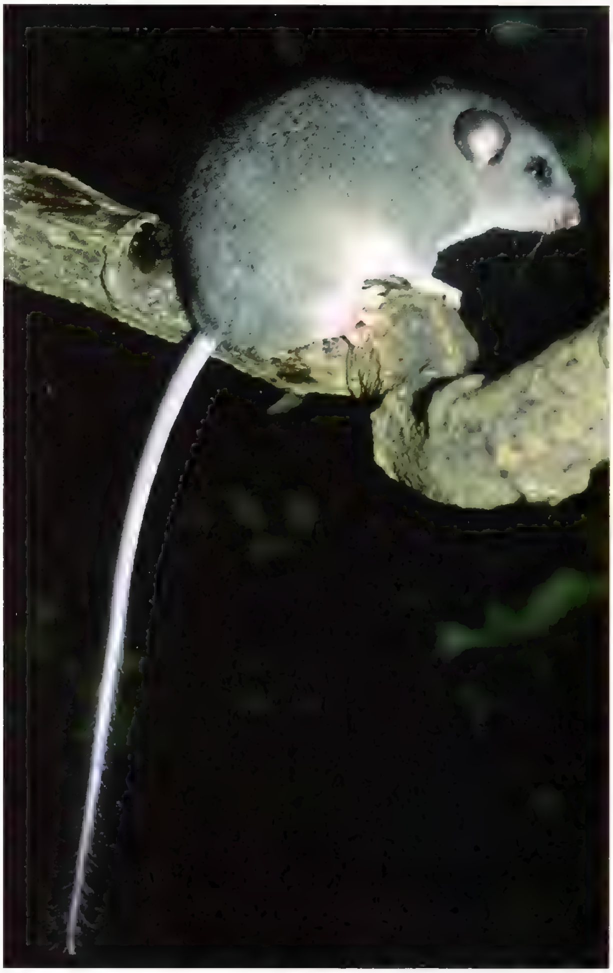

Fig. 2. Photograph of live *Eliurus carletoni* (FMNH 169718), a young adult male from the forest near the Andrafiabe Cave in the Réserve Spéciale d'Ankarana. The light colored ventral portion of the tail is slightly exaggerated by the photographic flashes. Photograph taken by Harald Schütz.

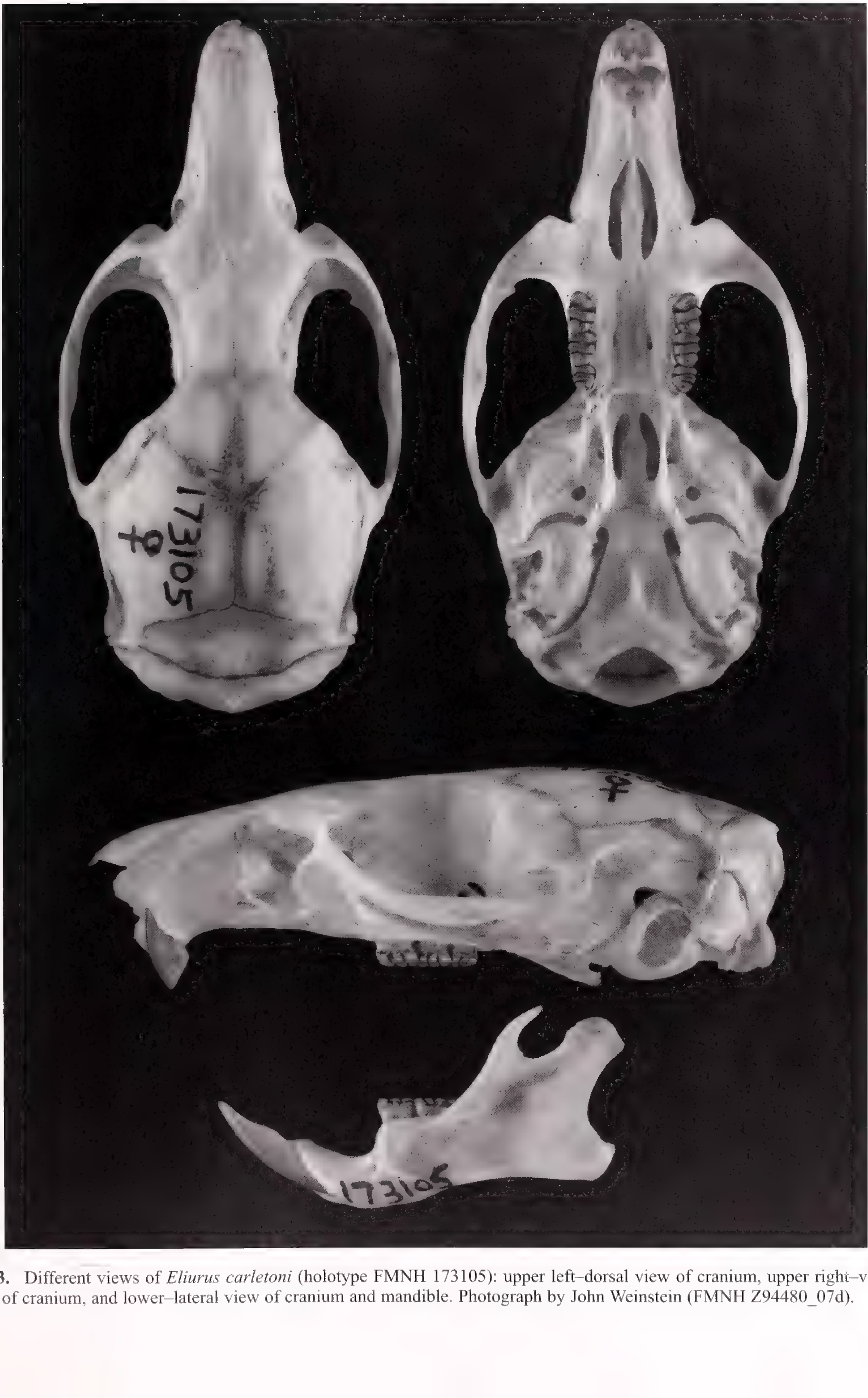

Fig. 3. Different views of *Eliurus carletoni* (holotype FMNH 173105): upper left–dorsal view of cranium, upper right–ventral view of cranium, and lower–lateral view of cranium and mandible. Photograph by John Weinstein (FMNH Z94480_07d).

Table. 1. Summary statistics (mean ± standard deviation, observed range, and sample size) for external morphological measurements of *Eliurus antsingy* from Bemaraha, *E. antsingy* from Namoroka, *E. carletoni* from Ankarana, *E. danieli* from Isalo, and *E. majori* from Montagne d'Ambre. See Materials and Methods for definitions of acronyms.

Variable	*E. antsingy* Bemaraha	*E. antsingy* Namoroka	*E. carletoni* Ankarana	*E. danieli* Isalo	*E. majori* Montagne d'Ambre
TOTL	354	329.2 ± 21.90 305–364, n=5	328.3 ± 9.07 318–335, n=3	335, 337	336.0 ± 14.62 322–365, n=7
HBL	160	146.8 ± 5.19 142–153, n=4	147.7 ± 4.04 143–150, n=3	150, 152	146.6 ± 4.18 141–154, n=6
TL	186	170.2 ± 15.42 153–195, n=5	174.3 ± 9.61 164–183, n=3	179, 195	179.1 ± 13.66 165–208, n=7
HFL	32	29.8 ± 1.26 28–31, n=4	28.8 ± 0.50 28–29, n=4	30, 32	28.5 ± 1.51 27–31, n=8
EL	26	24.8 ± 1.26 24–25, n=5	24.3 ± 0.96 23–25, n=4	26, 28	19.8 ± 1.49 17–21, n=8
WT	131	92.8 ± 6.55 87–101, n=4	94.8 ± 4.72 88–99, n=4	91, 100	79.5 ± 5.58 70–89, n=8

all other changes are silent): C189T, C201A, C270T, C312T, C321T, C522T, C585A, T598C, T678C, **T710C, C722T**, T768C, T837C, T849C, C879T, A945C, A978G, C1069T.

Referred specimens. Other specimens of *Eliurus carletoni* have been examined in this study, all from the RS d'Ankarana and collected by S. M. Goodman (except as noted). The following three specimens were obtained from the type locality: FMNH 173104 (SMG 12728), a young adult female, with partially fused basisphenoid suture, on 6 April 2002; FMNH 173106 (SMG 12833), a young adult male, with abdominal testes, with unfused basisphenoid suture, on 9 April 2002; FMNH 173109 (SMG 12848), an adult female, with largely fused basisphenoid suture, on 11 April 2002. An additional three specimens were taken from 2.6 km E Andrafiabe, in forest near Andrafiabe Cave, 12°55.9'S, 49°03.4'E; ca. 50 m above sea-level: FMNH 169718 (SMG 11928), a young adult male, with unfused basisphenoid suture, obtained on 22 January 2001; FMNH 169719 (SMG 11946), a young adult female, with unfused basisphenoid suture, on 24 January 2001; FMNH 169720 (SMG 11994), an adult scrotal male, with fused basisphenoid suture, on 26 January 2001. Two additional specimens were collected by Achille P. Raselimanana near the trail junction of routes to Matsaborimanga, Campement des Anglais, and Andafiabe, 10.0 km NW Mahamasina, ca. 12°53.2'S, 49°06.6'E; 100 m above sea-level: FMNH 173107 (SMG 12846), an adult female, with largely fused basisphenoid suture, on 11 April 2002; FMNH 173108 (SMG 12847), a young adult male, with unfused basisphenoid suture, on 11 April 2002. In addition, a number of incomplete cranial specimens referable to *E. carletoni* have been recovered pellets of the Madagascar Red Owl (*Tyto soumagnei*) collected at the RS d'Ankarana, Perte des Rivières (12°57.283'S, 49°7.627'E).

Etymology. This new species is named in honor of Dr. Michael D. Carleton of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. in recognition of his immense contributions to the field of rodent systematics. In particular, Dr. Carleton has worked extensively on the systematics and morphological evolution of Madagascar's native rodents.

Distribution. This species is currently only known from the RS d'Ankarana in the extreme northern portion of Madagascar (Fig. 1). Specimens obtained in the RS d'Analamerana and the Réserve Forestière de Loky-Manambato (Daraina region) may be referable to this taxon; future studies will address this question.

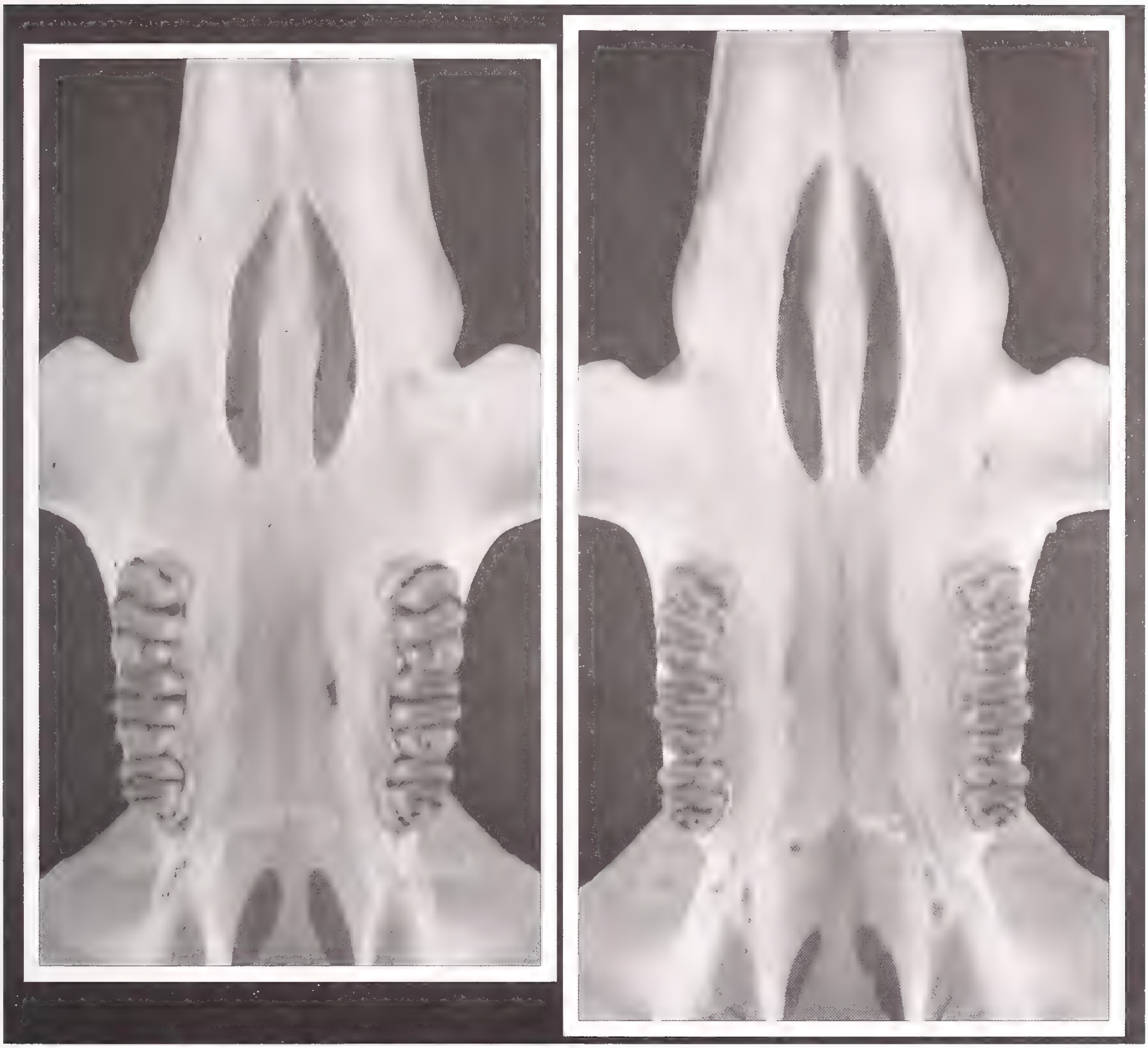

Fig. 4. Comparison of incisive foramen and molar toothrows – (right) in the holotype of *Eliurus carletoni* (FMNH 173105) from the Réserve Spéciale d'Ankarana and (left) *E. antsingy* from the Parc National de Bemaraha (FMNH 172271). Note that this structure is reduced in length and width in the former species, as well as the palatine process, which is thick and short. Photograph by John Weinstein (FMNH Z94480_08d).

Description. Overall body hair texture soft and relatively fine. Dorsum cover hairs 7–9 mm in length over middle rump and 5–6 mm at the level of the nape. Cover hairs of dorsum largely bi-colored with proximal two-thirds dark brown and distal one-third medium buff, although some hairs tipped with faint dusky brown. Guard hairs dark brown to blackish. The overall coloration of the upperparts, including forehead and face, is a dark agouti with a diffused mid-dorsal line that is notably darker than the surrounding fur. In several individuals, this band broadens towards the rump. Fur coloration of lower legs approaches a lighter tannish-brown. In a few individuals (FMNH 173107, 173108), the dorsal pelage coloration is slightly lighter, with the forehead, face, and lower legs being tannish-brown. Along mid-portion of body, the limit between the dorsal and ventral pelage is relatively well demarcated. The coloration of the ventrum is variable and ranges from being nearly entirely white (FMNH 169719, 173107, 173108), being largely white with a diffusion of gray towards the throat and base of limbs (FMNH 173109), to being broadly diffused with light gray and having dusky brown at the base of the limbs (as in holotype FMNH 173105). A diffuse dusky-brown band extends over the mid-portion of the dorsal tarsus surface and prox-

Table. 2. Summary statistics (mean ± standard deviation, observed range, and sample size) for craniodental measurements of adult *Eliurus antsingy* from Bemaraha, *E. antsingy* from Namoroka, *E. carletoni* from Ankarana, *E. danieli* from Isalo, and *E. majori* from Montagne d'Ambre. See Materials and methods for explanation of acronyms and age classes. Measurements for two of the *E. antsingy* specimens (MNHN 1966.2220, 1966.2222) were taken from CARLETON & GOODMAN (2007).

Variable	*E. antsingy* Bemaraha	*E. antsingy* Namoroka	*E. carletoni* Ankarana	*E. danieli* Isalo	*E. majori* Montagne d'Ambre
ONL	43.2 ± 1.14 41.9–44.1, n=3	41.0 ± 1.40 39.3–42.5, n=5	40.2 ± 0.48 39.5–40.6, n=4	39.1, 40.6	36.9 ± 0.68 36.1–38.0, n=7
ZB	21.2 ± 0.51 20.8–21.8, n=3	19.3 ± 0.62 18.4–20.3, n=6	19.7 ± 0.31 19.4–20.0, n=3	18.9, 19.1	18.8 ± 0.42 18.3–19.4, n=7
BBC	16.1 ± 0.26 15.8–16.3, n=3	15.1 ± 0.20 14.9–15.4, n=6	15.1 ± 0.25 14.8–15.4, n=4	14.6, 15.1	14.4 ± 0.18 14.1–14.7, n=8
IOB	6.1 ± 0.15 5.9–6.2, n=3	5.9 ± 0.14 5.7–6.1, n=6	5.6 ± 0.08 5.5–5.7, n=4	5.3, 5.8	5.2 ± 0.21 4.9–5.5, n=8
LR	14.9 ± 0.21 14.7–15.1, n=3	13.2 ± 0.55 12.7–14.1, n=5	12.6 ± 0.24 12.2–12.7, n=4	12.2, 13.3	11.8 ± 0.37 11.5–12.6, n=7
BR	7.4 ± 0.06 7.4–7.5, n=3	6.8 ± 0.23 6.4–7.0, n=6	7.0 ± 0.17 6.7–7.1, n=4	7.0, 7.4	6.9 ± 0.07 6.8–7.2, n=8
PPL	15.2 ± 0.61 14.7–15.9, n=3	14.3 ± 0.61 13.7–15.0, n=6	14.3 ± 0.25 14.0–14.6, n=4	13.8, 13.8	12.8 ± 0.60 12.0–13.6, n=8
LBP	7.8 ± 0.10 7.7–7.9, n=3	8.1 ± 1.06 7.3–10.2, n=6	7.6 ± 0.21 7.3–7.9, n=4	7.7, 7.8	7.4 ± 0.43 6.8–8.0, n=8
PPB	6.1 ± 0.06 6.0–6.1, n=3	5.5 ± 0.13 5.3–5.6, n=6	5.5 ± 0.22 5.2–5.7, n=4	5.7, 5.9	5.6 ± 0.15 5.4–5.8, n=8
LIF	6.7 ± 0.10 6.6–6.8, n=3	5.7 ± 0.52 4.7–6.0, n=6	5.2 ± 0.22 4.9–5.4, n=4	5.3, 5.4	5.1 ± 0.32 4.6–5.6, n=8
BIF	2.9 ±0.21 2.7–3.1, n=3	2.4 ± 0.22 2.0–2.6, n=6	2.6 ± 0.10 2.4–2.6, n=4	2.7, 2.7	2.2 ± 0.21 2.0–2.5, n=8
LD	11.8 ± 0.56	10.9 ± 0.89	10.7 ± 0.24	9.8, 10.1	9.8 ± 0.21

Table. 2. (pursuit).

Variable	***E. antsingy* Bemaraha**	***E. antsingy* Namoroka**	***E. carletoni* Ankarana**	***E. danieli* Isalo**	***E. majori* Montagne d'Ambre**
	11.3–12.4, n=3	10.1–12.5, n=6	10.4–10.9, n=4		9.4–10.0, n=7
BM1s	8.2 ± 0.15 8.0–8.3, n=3	7.5 ± 0.14 7.3–7.7, n=6	7.5 ± 0.26 7.3–7.8, n=4	7.7, 7.7	7.5 ± 0.25 7.0--7.7, n=7
DAB	6.3 ± 0.26 6.0–6.5, n=3	5.7 ± 0.21 5.5–6.0, n=6	5.6 ± 0.17 5.4–5.8, n=4	5.6, 5.8	5.3 ± 0.18 5.0–5.5, n=8
BZP	3.7 ± 0.57 3.2–4.3, n=3	3.9 ± 0.34 3.5–4.5, n=6	3.6 ± 0.15 3.4–3.7, n=4	3.8, 3.8	3.2 ± 0.18 3.0–3.5, n=8
BOC	9.6 ± 0.10 9.5–9.7, n=3	8.8 ± 0.20 8.5–9.1, n=6	8.9 ± 0.17 8.7–9.1, n=4	8.6, 8.7	8.3 ± 0.20 8.1–8.6, n=8
LM1-3	5.8 ± 0.15 5.7–6.0, n=3	5.6 ± 0.23 5.3–5.9, n=6	5.6 ± 0.14 5.4–5.7, n=4	5.9, 6.2	5.9 ± 0.20 5.6–6.3, n=8
WM1	1.6 ± 0.10 1.5–1.7, n=3	1.6 ± 0.08 1.4–1.6, n=6	1.6 ± 0.06 1.5–1.6, n=4	1.6, 1.7	1.7 ± 0.07 1.6–1.8, n=8

imal metatarsus; the balance of these structures is dominated by light-colored fur intermixed with light brown. Relatively well-developed white ungual tufts at base of claws.

Caudal tail tuft prominent over distal half of length, tuft hairs becoming gradually longer toward the tip and measuring about 10–13 mm long near the terminal portion. Tail fur notably mono-colored, dark blackish-brown along complete length. The only exception is FMNH 173108, which has a 7 mm wide largely white-haired section starting about 30 mm from the terminal tip. Proximal half of tail covered with short black hairs that sparsely cover the caudal scales. Ventral tail scales distinctly rectangular-shaped and on the dorsal surface dark brownish and on the ventral surface light gray at base merging to dark brownish distally. One animal with a short bobbed tail (FMNH 169720) has a distorted dark blackish-brown terminal tuft, but there is no evidence of white replacement hair.

Hind feet short and broad; absolutely and relatively smaller than in *E. antsingy* from Bemaraha (FMNH 172721). Plantar pads six and arranged as characteristic of the genus (Carleton 1994, his fig. 2). Pinnae relatively short and not as long as *E. antsingy* from Bemaraha (Table 1); color dark brown externally and sparsely clothed with fine light-colored hairs.

Cranium the size of other moderately large members of the genus (ONL = 39.5–40.6 mm), but more diminutive than *E. antsingy* from Bemaraha (ONL = 41.9–44.1 mm) and smaller on average than *E. antsingy* (ONL = 39.3–42.5 mm) from Namoroka. Similar in overall profile shape to *E. antsingy,* but skull less sharply arched towards occiput (Fig. 3). Rostrum proportionately shorter (LR/ONL = 30.9–31.3%), as compared to *E. antsingy* from Bemaraha (LR/ONL = 34.9%) and all other members of the genus. Braincase not notably rounded as in, for example, *E. danieli* or other members of the *E. majori* group. Subsquamosal fenestra notably reduced, similar to *E. ants-*

Table. 3. Factor loadings from principal component analyses of log transformed craniodental measurements of specimens of adult *Eliurus antsingy* (Bemaraha and Namoroka), *E. carletoni, E. danieli*, and *E. majori* (Montagne d'Ambre). For this analysis, a graphical representation of the first two factors is presented in Fig. 5. On the basis of ANOVA analyses, two craniodental variables, LBP and WM1, showed no significant differences across taxa and were not included in the PCA analysis.

	Factor 1	Factor 2	Factor 3
ONL	-0.944	0.254	0.018
ZB	-0.869	-0.002	-0.048
BBC	-0.939	0.027	0.114
IOB	-0.883	0.215	0.172
LR	-0.944	-0.005	-0.186
BR	-0.457	-0.543	-0.420
PPL	-0.901	0.211	0.119
PPB	-0.602	-0.639	0.0343
LIF	-0.730	-0.472	0.197
BIF	-0.639	-0.421	0.386
LD	-0.831	0.386	-0.214
BM1	-0.618	-0.617	-0.032
DAB	-0.931	0.071	-0.083
BZP	-0.545	0.447	-0.439
BOC	-0.923	-0.125	0.247
LM1-3	0.108	-0.847	-0.254
Eigenvalues	9.842	3.519	1.554
Proportion of total variation explained	54.7%	74.2%	82.9%

ingy from Bemaraha, without exposing the interior braincase. Hamular process of the squamosal reduced and stout, similar to that in *E. antsingy* from Bemaraha. Zygomatic arches not notably heavy, although the zygomatic plates are proportionately stouter as compared to other members of the genus of similar ONL length. Nasolacrimal capsule more inflated and nasolacrimal foramen closer to zygomatic notch than in *E. antsingy* from Bemaraha.

Incisive foramina bluntly pointed on their posterior and anterior ends; notably short (LIF/LD = 47.1–49.5%) for members of the genus; in *E. antsingy* from Bemaraha the LIF/LD = 56% (Fig. 4). Posterior palatine foramina oblong ovals, situated within the maxillary-palatine suture at the level of the M1-M2. Palatine process stout and short. Supernumerary palatal foramina occurring in the palatine bones, but minute in size and irregularly formed; in the holotype these occur on the animal's left side at the level of M2-M3 and on the right side in the central portion of M3. No posterolateral palatal foramen. Posterior margin of the bony palate terminates at the posterior ends of the third molars. The anterior portion of the mesopterygoid fossa is broad, U-shaped, and extending distally without a constriction in the central winged portions of the pterygoid process. Auditory bullae relatively small for the genus; from ventral view the ectotympanic covering only a portion of the petrosal part of auditory bullae and a small portion of the periotic.

Anterior enamel surface of upper and lower incisors dull yellowish-orange. Alveolus of lower incisor terminating at the level of the coronoid process and below the sigmoid notch. The base of the incisor root forming slight rise on mandibular ramus but not a capsular process. Toothrows not particularly elongated (LM1-3 = 5.4–5.7 mm) and relative to cranial size, in proportion to those of *E. myoxinus* and *E. tanala* Major, 1896 (CARLETON 1994, Appendix 2). Molars robust with trilaminar configuration on planar surface, typical of other members of this genus; upper and lower first and second molars about equal in length and both notably longer than third molars.

Morphological comparisons. On the basis of numerous morphological traits, *E. carletoni* is placed along with *E. antsingy* from Namoroka and Bemaraha in the same species assemblage (CARLETON & GOODMAN, 2007). Given the morphological uniqueness of this species complex, as outline by CARLETON et al. (2001) and CARLETON & GOODMAN (2007), our comparisons here are largely confined to other populations within the group. The northern population of *E. majori*, occurring on Montagne d'Ambre, is also included, because this is geographically the closest known moderately sized *Eliurus*. Further comparisons are also made to *E. danieli* from transitional dry/humid forests of the PN de l'Isalo in the central west. Both *E. majori* and *E. danieli* are included within the *E. majori* group, which CARLETON & GOODMAN (2007) allied with the *E. antsingy* group (see below).

In general, the dorsal pelage coloration of *E. carletoni* is similar to *E. antsingy*; however, the dorsum cover hairs towards the middle rump tend to be slightly longer in *E. antsingy* (9–11 mm) as compared to *E. carletoni* (7–9 mm). Specimens of *E. majori* from Montagne d'Ambre have distinctly dark slate gray dorsums and a denser and more svelte dorsal pelage and those of *E. danieli* have bright plumbeous gray cover hairs. The ventral pelage of *E. carletoni* varies from only being slightly tinged with white in FMNH 173105 (the holotype), to being largely white-bellied. However, in all cases *E. carletoni* has more whitish-colored fur on the belly than *E. antsingy* from Bemaraha (FMNH 172721), whereas all eight of the skin preparations of *E. antsingy* from Namoroka have white venters. Both *E. carletoni* and *E. antsingy* have mono-colored tails, generally with dark-blackish brown fur along the complete length, and the caudal tuft occupies the distal half of the tail. Some individuals of *E. antsingy* from Namoroka have notably light brown tails and reduced caudal tufts; these include both young adults (FMNH 178591, 178593) and full adults (FMNH 178592) and this difference does not appear to be age related. Amongst the specimens of *E. carletoni* there is one anomalous case (FMNH 169720), which has a small white band along its length. Other species of *Eliurus* with largely mono-colored dark-blackish brown tails include *E. myoxinus* and *E. webbi* Ellerman, 1949, which can be distinguished from *E. carletoni* by the tail length and pilosity, as well as numerous craniodental characters (Carleton 1994, 2003; Carleton et al. 2001).

Eliurus carletoni is distinctly smaller and lighter than *E. antsingy* from Bemaraha (FMNH 172271), but overlaps in all external measurements with specimens of *E. antsingy* from Namoroka (Table 1). The cranium of *E. carletoni* (ONL = 39.5–40.6 mm) approximates the size of other moderately large members of the genus (Carleton 1994), including *E. danieli* and *E. majori*, but it is notably smaller than *E. antsingy* from Bemaraha (ONL = 41.9–44.1 mm) and smaller on average than *E. antsingy* (ONL = 39.2–42.5 mm) from Namoroka (Table 2). The rostrum is proportionately shorter in *E. carletoni* (LR/ONL = 30.9–31.3%) as compared to *E. antsingy* from Bemaraha (LR/ONL = 34.2–35.1%) and from Namoroka (LR/ONL = 32.3–33.2%), as well as most other members of the genus (calculated from descriptive statistics in Carleton, 1994, Appendix 2): *E. minor* (LR/ONL = 33.3%), *E. myoxinus* (LR/ONL = 34.1%), *E. majori* (LR/ONL = 34.4%), *E. tanala* (LR/ONL = 36.0%), *E. webbi* (LR/ONL = 35.3%), and *E. petteri* Carleton, 1994 (LR/ONL = 35.3%).

The hamular process of the squamosal notably reduced within the *E. antsingy* group; in contrast to *E. danieli* and *E. majori* (from Montagne d'Ambre) in which the hamular process is elongated and associated with a more prominent subsquamosal foramen. *Eliurus carletoni* has a notably short (LIF/LD = 47.1–49.5%) and bluntly pointed incisive foramen, as compared to *E. antsingy* from Bemaraha (LIF/LD = 56%; Fig. 4). The palatine process in *E. carletoni* is generally thick and short, particularly in

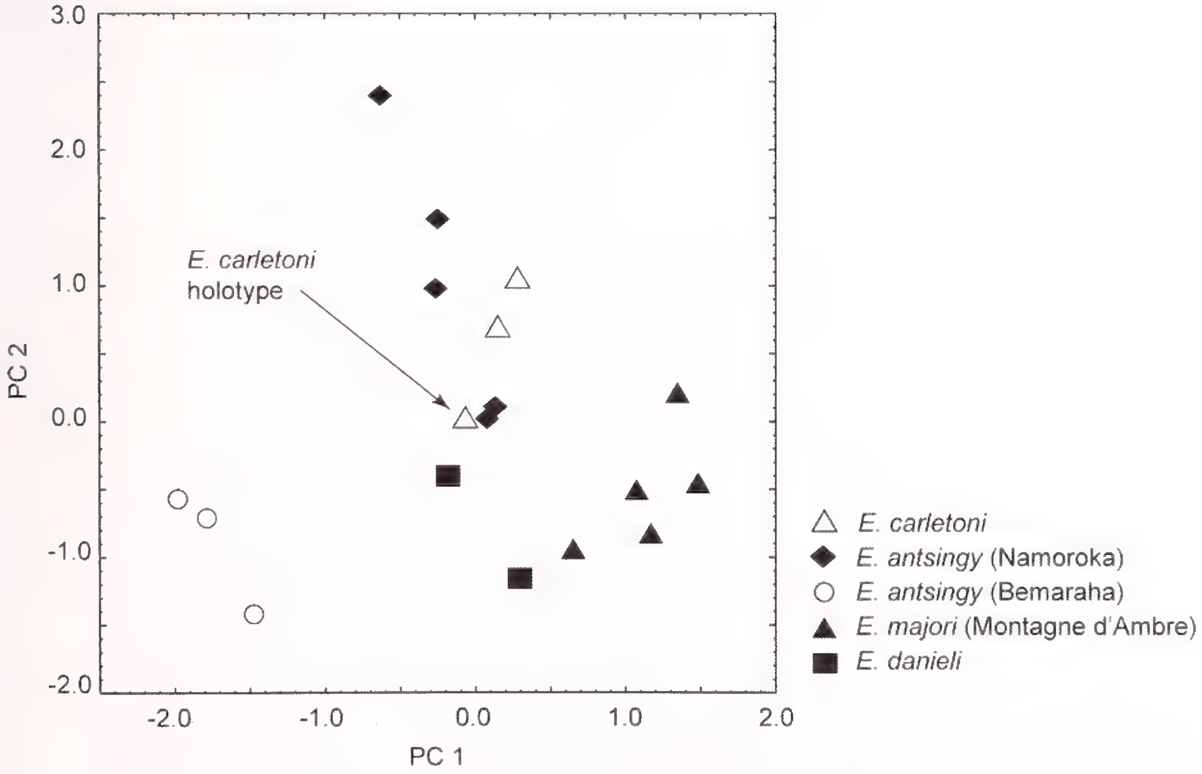

Fig. 5. Projections of factor 1 (x-axis) and factor 2 (y-axis) in principal component analysis on 16 ln-transformed craniodental variables of *Eliurus* spp. Loadings of variables on each axis are shown in Table 3.

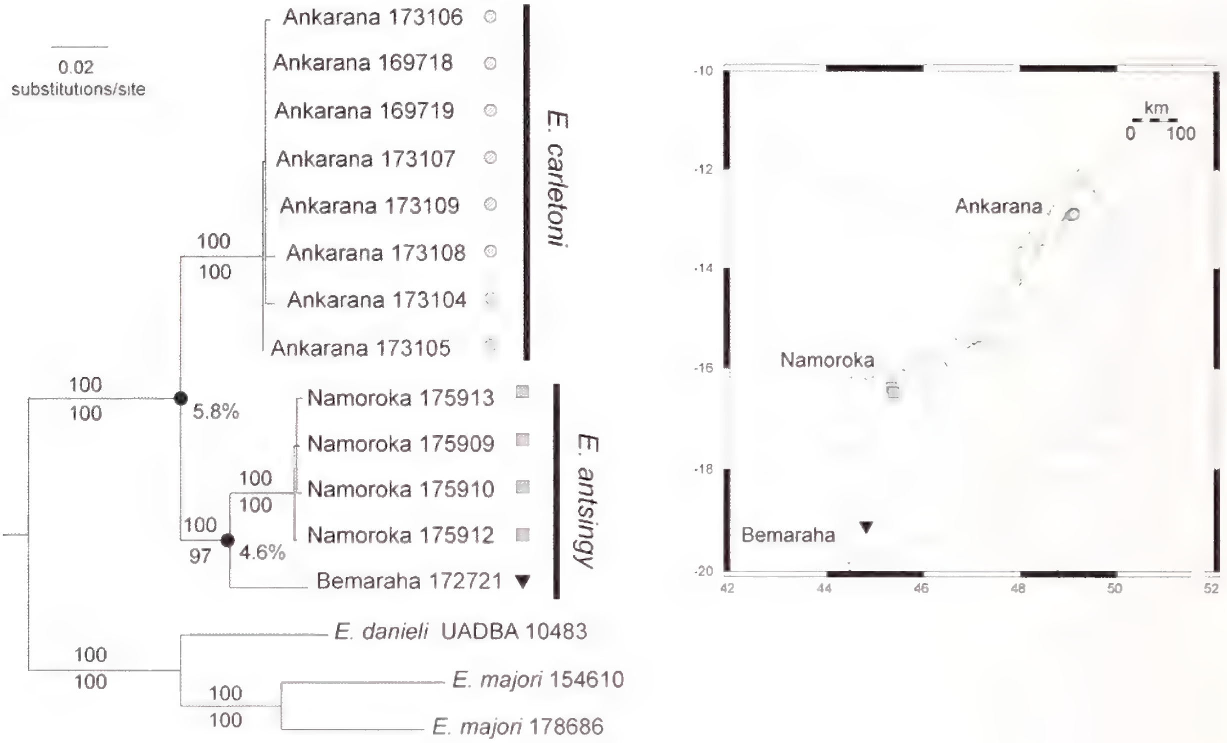
0.02
substitutions/site
Ankarana 173106
Ankarana 169718
Ankarana 169719
Ankarana 173107
Ankarana 173109
Ankarana 173108
Ankarana 173104
Ankarana 173105
E. carletoni
100
100
100
100
5.8%
Namoroka 175913
Namoroka 175909
Namoroka 175910
Namoroka 175912
Bemaraha 172721
E. antsingy
100
100
100
97
4.6%
E. danieli UADBA 10483
E. majori 154610
E. majori 178686
100
100
100
100
km
0 100
Ankarana
Namoroka
Bemaraha
-10
-12
-14
-16
-18
-20
42
44
46
48
50
52

Fig. 6. The maximum-likelihood phylogeny inferred from analysis under the best-fit model of nucleotide substitution for the cyt-*b* data (GTR + I, no clock; -lnL = 3137.31). The tree is rooted with sequences of *Eliurus danieli* and two *E. majori*. The ingroup consists of specimens referred to *E. antsingy* or *E. carletoni*. Terminal branches within the ingroup are labeled with collecting localities shown in the map (right), followed by the museum (FMNH, unless otherwise noted) voucher number. Numbers above and below branches refer to maximum-likelihood and parsimony bootstrap support, respectively. The divergence between populations (ML-corrected) is shown next to circles at each interpopulation node.

comparison to the narrow and relatively long structure in *E. antsingy* and members of the *E. majori* group. The posterior palatine foramina are consistently the same size and are positioned within the maxillary-palatine suture at the level of the M1-M2 for all members of the *E. majori* and *E. antsingy* groups. The external portion of the auditory bullae of *E. carletoni* is notably smaller than in *E. antsingy* from Bemaraha (DAB 5.4–5.8 mm vs. 6.0–6.5 mm), whereas animals from Namoroka largely overlap *E. carletoni* in this measurement (DAB 5.5–6.0 mm).

In all specimens of *E. antsingy* and *E. carletoni*, the molars have a robust trilaminar configuration and the anterior enamel surface of upper and lower incisors are dull yellowish-orange. The position of the lower incisor root with respect to the coronoid process is likewise consistent across members of this group. The toothrows in *E. carletoni* are shorter than *E. antsingy* from Bemaraha (LM1-3 = 5.4–5.7 mm vs. 5.7–6.0 mm), but overlap with those in specimens from Namoroka (LM1-3 = 5.3–5.9 mm). Members of the *E. antsingy* group have proportionately shorter molar rows relative to cranial size than members of the *E. majori* group: *E. carletoni* LM1-3/ONL = 13.7–14.0%, *E. antsingy* from Bemaraha LM1-3/ONL = 13.6%, *E. danieli* LM1-3/ONL = 15.1–15.3%, and *E. majori* from Montagne d'Ambre LM1-3/ONL = 15.5–16.6%. Members of the *E. antsingy* species assemblage have the upper and lower third molars subequal in length to the first and second molars. The same condition is found in *E. danieli*, while the three molars are largely the same size in *E. majori* from Montagne d'Ambre.

Principal Component Analysis of craniodental measurements (Fig. 5) shows complete separation of *E. antsingy* taken in Bemaraha from *E. carletoni* and *E. majori* from Montagne d'Ambre; although there is broad overlap between *E. carletoni* and *E. antsingy* from Namoroka. The factor loadings for this analyses (Table 3) indicates that the majority of variables for factor 1 and coronal length of maxillary toothrow (LM1-3) for factor 2 showed heavy negative loadings. Factor 1 explained 54.7% of the total variation, factor 2 an additional 19.5%, and factor 3 an-

Table. 4. Unreversed synapomorphies (inferred from parsimony optimization on the tree shown in Fig. 6) from the cyt-*b* gene that diagnose *Eliurus carletoni, E. antsingy,* and populations of *E. antsingy* from Namoroka and Bemaraha.

	E. carletoni				***E. antsingy* (Namoroka + Bemaraha)**		
Character No.	Change	Codon position	Effect	Character No.	Change	Codon position	Effect
189	C→T	3	silent	45	C→T	3	silent
201	C→A	3	silent	120	C→T	3	silent
270	C→T	3	silent	243	T→C	3	silent
312	C→T	3	silent	315	T→C	3	silent
321	C→T	3	silent	438	T→C	3	silent
522	C→T	3	silent	567	T→C	3	silent
585	C→A	3	silent	591	A→G	3	silent
598	T→C	1	silent	696	C→A	3	silent
678	T→C	3	silent	715	C→T	1	silent
710	T→C	2	Met→Thr	798	C→T	3	silent
722	C→T	2	Ser→Phe	894	T→C	3	silent
768	T→C	3	silent	906	C→T	3	silent
837	T→C	3	silent	963	T→C	3	silent
849	T→C	3	silent	969	A→G	3	silent
879	C→T	3	silent	1038	C→T	3	silent
945	A→C	3	silent	1083	T→C	3	silent
978	A→G	3	silent				
1069	C→T	1	silent				

	***E. antsingy* (Namoroka)**				***E. antsingy* (Bemaraha)**		
Character No.	Change	Codon position	Effect	Character No.	Change	Codon position	Effect
67	A→G	1	Thr→Ala	48	C→A	3	Asn→Lys
138	C→T	3	silent	108	C→A	3	silent
198	C→T	3	silent	207	T→C	3	silent
201	C→T	3	silent	273	C→T	3	silent
240	C→T	3	silent	279	C→T	3	silent
280	T→C	1	silent	303	A→T	3	silent
364	A→G	1	Thr→Ala	345	A→G	3	silent
426	G→A	3	silent	369	A→G	3	silent
471	A→G	3	silent	396	A→G	3	silent
489	A→G	3	silent	528	C→T	3	silent
582	A→G	3	silent	585	C→T	3	silent
621	C→T	3	silent	654	C→T	3	silent
630	C→T	3	silent	687	C→T	3	silent
999	C→T	3	silent	724	C→T	1	silent
1068	C→T	3	silent	831	T→C	3	silent
1095	T→C	3	silent	1078	G→A	1	Ala→Thr
1122	C→T	3	silent	1093	T→C	1	Phe→Leu
				1124	A→G	2	Asn→Ser
				1138	A→G	1	Asn→Asp

other 8.7%. Whereas it is the case that *E. carletoni* and *E. antsingy* from Namoroka showed broad morphological overlap in the PCA, based on the molecular phylogeny (see next section) these two populations are not sister taxa within the *E. antsingy* species group.

Molecular variation and phylogeny. There were 6 unique cyt-*b* haplotypes among the 8 specimens from Ankarana, and nucleotide diversity (π) among them was 0.003. Each of the specimens from the Namoroka population had a unique haplotype, and nucleotide diversity within this population was also 0.003. Average sequence divergence (corrected for within-population polymorphism; Nei 1987, eq. 10–21) was 4.4% (ML-corrected divergence = 4.6%) between the Namoroka and Bemaraha populations and 4.9% (5.8% ML-corrected) between Ankarana and the two southern populations.

Phylogenetic analysis of the cyt-*b* dataset using parsimony resulted in three minimum-length trees (L = 350; CI = 0.80; RI = 0.86). The strict-consensus of these trees is less resolved than but entirely consistent with the topology resulting from a maximum-likelihood analysis of this dataset under its best-fit model (GTR+I, no clock; Fig. 6). Two well-supported clades are apparent within *E. antsingy* when this tree is rooted with *E. danieli* and two individuals of *E. majori*. The first includes the specimens from Ankarana, the second comprises specimens from Namoroka and Bemaraha. When character state changes are optimized on this phylogeny, 18 unreversed synapomorphies can be mapped to the branch subtending the Ankarana specimens (*E. carletoni*); two of these result in amino acid substitutions. An additional 16 unreversed synapomorphies (all silent changes) can be mapped to the branch subtending *E. antsingy* from Namoroka and Bemaraha (Table 4).

Ecological notes. All of the specimens of *E. carletoni* used in this study were collected in the forests of the Ankarana Massif, specifically the RS d'Ankarana in northern Madagascar (Fig. 1). This region lies on a block of karstic limestone that was formed during the Jurassic and subsequently uplifted (Cardiff & Befourouack 2003). The weathering of the exposed limestone surface has formed the pinnacle karst known in Malagasy as *tsingy,* which is characteristic of the Ankarana Massif, as well as the *tsingy* habitat at Bemaraha and Namoroka.

The zone surrounding the Ankarana Massif receives slightly less than 2000 mm of rainfall annually, of which most falls between the months of December to April, resulting in a prominent seven-month dry season (Fowler et al. 1989; Hawkins et al. 1990). The deep canyons, which provide protection from the sun and desiccating wind, and underground streams passing close to or resurging at ground level, result in relatively mesic forest conditions within these formations. It is in such areas that *E. carletoni* has been found during biological inventories.

On the basis of trap captures set both on the ground and along lianas, *E. carletoni* can be characterized as a primarily scansorial forest-dwelling inhabitant of the dry deciduous habitats of the Ankarana Massif. It has been trapped in pristine and disturbed forests, generally associated with *tsingy* rock formations, and on the ground, branches and vines. Some notes associated with captured animals help to characterize the different microhabitats it occupies: "…at base of *tsingy*. Trap on ground between rocks and just above water source" (FMNH 169718); "at base of *tsingy*. Trap 1.75 m off ground on 5 cm diam[eter] liana arching over ground to mid-canopy" (FMNH 169719); "Trap on ground in narrow passage between two rocks – resting on *tsingy*" (FMNH 169720); "Trap on ground along large fallen and rotten tree trunk next to *tsingy* wall" (FMNH 173104); "Trap about 1 m off the ground on 20 cm diam[eter] fallen tree trunk" (FMNH 173106); and "In disturbed deciduous forest. Not within 500 m of *tsingy* formation" (FMNH 173107, 173108).

On the basis of rapid inventory information it is difficult to infer many details on the reproductive behavior and seasonality of *E. carletoni*, but a few observations can be presented. Individuals collected in late January 2001 included a young adult male and a female (FMNH 169718, 169719) that were not in reproductive condition, as well as an adult male (FMNH 169720) with large scrotal testes and convoluted epididymides. A series of animals captured during early April 2002 included one adult male that was not in reproductive condition (FMNH 173106); three females each of which had large mammae but no embryos, and one of which had discernable placental scars (one in each the left and right uterine horns) (FMNH 173104, 173107, 173109); and a male with partially scrotal testes, (measuring 5 x 5 mm) and slightly convoluted epididymides (FMNH 173108).

A recent study on the dietary habits of the owl *Tyto soumagnei* within the RS d'Ankarana, found that this raptor feeds extensively on *E. carletoni* (which was identified as *E. antsingy* in that study). Across several different seasons and years, *E. carletoni* comprised 22.1% of the minimum number of individuals and 49.8% of the biomass consumed by this owl (Cardiff & Goodman 2008). At Ankarana, other than the bat fauna (14 species; Goodman et al. 2005), the diversity of mammals weighing less than 100 gm is rather limited. No other species of native rodent has been captured at this site, but two species of introduced rodent (*Rattus rattus* [Linnaeus, 1758] and *Mus musculus* Linnaeus, 1758) occur here. In addition, a shrew (*Suncus madagascariensis* [Coquerel, 1848]), a small shrew-tenrec (*Microgale brevicaudata* G. Grandidier, 1899), and a mouse lemur (*Microcebus tavaratra* Rasoloarison, Goodman & Ganzhorn, 2000) are known from the reserve. Previous reports of *E. myoxinus* in Ankarana (NICOLL & LANGRAND 1989) have not been substantiated during recent biological inventories (CARLETON et al. 2001; GOODMAN, unpublished data).

4. DISCUSSION

CARLETON & GOODMAN (2007) examined morphological variation in described members of the genus *Eliurus* and divided these animals into five different groups. Two of the species assemblages important for the current discussion include the *Eliurus majori* group (comprising *E. majori*, *E. penicillatus* Thomas, 1908, and *E. danieli*) and the *Eliurus antsingy* group (comprising *E. antsingy*, and the newly described *E. carletoni* presented herein). On the basis of several external morphological and craniodental characteristics, these authors suggested that these two species groups might be more closely related to each other than either is to any other species of *Eliurus*. This hypothesis remains to be critically tested with molecular data, but preliminary results based on mitochondrial cyt-*b* data (JANSA, unpublished data) lend credence to this suggestion.

As currently understood, members of the *E. antsingy* group have a broad but disjunct geographic distribution across northern Madagascar, and occur in zones of lowland deciduous forest resting on limestone outcrops (Fig. 1). The type locality of *E. antsingy* is the Bemaraha Plateau in central west Madagascar, a limestone formation dating from the mid-Jurassic. In their description of this taxon, CARLETON et al. (2001) tentatively assigned *Eliurus* specimens from the Namoroka Massif – another *tsingy* limestone area 300 km further to the north – to *E. antsingy*. However, they noted that the animals from Namoroka were consistently smaller and had whiter ventral pelage than those from Bemaraha; these differences are upheld in the larger sample from Namoroka presented herein. Based on our molecular phylogeny of the *E. antsingy* species group (Fig. 6), the Namoroka animals are the sister taxon of the animal from Bemaraha, but the two populations differ by an average of 4.7% (ML-corrected) sequence divergence, and there are several fixed changes in the cyt-*b* gene that uniquely characterize each (Table 4). Therefore, these two populations could be considered two distinct species, or they may simply represent extremes of variation in a contiguous population. Our Bemaraha samples of *E. antsingy* come from the southern end of this approximately 100 km limestone formation and additional material from the unsampled *tsingy* habitat in the northern portion of this formation could harbor populations that will be critical for assessing the species status of the Bemaraha and Namoroka populations, which are here conservatively retain as the single species *E. antsingy*.

The *Eliurus* specimens from the Ankarana Massif – described here as *E. carletoni* – as well as a large-bodied *Eliurus* from the Forêt d'Ambilondambo (Daraina) were collected after CARLETON et al. (2001) published their description of *E. antsingy*. CARLETON & GOODMAN (2007) tentatively assigned these specimens to *E. antsingy* based on morphometric comparisons, but they called for additional collections from intermediate localities as well as genetic data to test this conclusion. Although we lack critical specimens from new locales, the application of molecular data to existing specimens clearly shows that the Ankarana population is reciprocally monophyletic relative to *E. antsingy* from Namoroka and Bemaraha, and that the two clades differ by 5.8% (ML-corrected) sequence divergence. In addition, the two species are diagnosable by several fixed changes in the cyt-*b* gene (Table 4). Additional collections from limestone areas – such as Ankara and Kelifely – between Namoroka and the northern portion of the island will help to resolve whether these two populations are genetically isolated. However, the lack of gene flow and high degree of molecular divergence between them apparent in this study, leads us to recognize the Ankarana population as a new species, *E. carletoni*. We note that specimens from Daraina are morphologically very similar to *E. carletoni* and may be assignable to this species as well. Ongoing morphological and molecular studies will help resolve this as well as other pressing questions in *Eliurus* systematics.

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Zusammenfassung. Die Nager-Art *Eliurus antsingy* (Nesomyinae) ist aktuell aus einigen disjunkten Kalkstein-Regionen in trockenen Tiefland-Waldgebieten im nördlichen und westlichen Madagaskar bekannt. Frühere Untersuchungen haben morphologische Unterschiede zwischen Individuen aus verschiedenen isolierten Populationen festgestellt, sahen aber alle als Angehörige derselben Art an. In der vorliegenden Untersuchung überprüfen wir die morphologische und genetische Variabilität innerhalb von und zwischen Populationen von *E. antsingy*, mit Schwerpunkt auf dem Status der Population der Réserve Spéciale d'Ankarana im äußersten Norden der Insel. Während eine Unterscheidung der Population in Ankarana von der ihr nächst vorkommenden ~500 km südlich (Namoroka) nicht möglich ist, unterschieden sich beide Populationen in morphologischen Merkmalen von der der Typuslokalität (Bemaraha) der Art. Im Gegensatz dazu bestehen zwischen allen drei Populationen deutliche genetische Unterschiede. Die phylogenetische Analyse dieser Daten deutet darauf hin, dass die beiden morphologisch ähnlichen Formen keine Schwester-Taxa sind. Auf der Grundlage dieser Ergebnisse sehen wir die Tiere der Réserve Spéciale d'Ankarana als neue Art an, fassen aber diejenigen aus den beiden anderen untersuchten Populationen wegen nicht ausreichend großer Stichproben vorläufig weiterhin als *E. antsingy* auf.

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APPENDIX

Specimens Examined of *Eliurus*

Listed below are specimens that formed the basis for the study's morphological comparisons. FMNH numbers in bold indicate specimens also used in the molecular study. Abbreviations for protected areas in Madagascar are: PN, Parc National; RNI, Réserve Naturelle Intégrale; RS, Réserve Spéciale.

Eliurus antsingy: Mahajanga Province: Antsingy forest near Bekopaka, ca. 19°07.5'S, 44°49.0'E (MNHN 1966.2220, 1966.2222); PN de Bemaraha, 3.5 km E Bekopaka, near Tombeau Vazimba, 100 m, 19°08.4'S, 44°49.7'E (FMNH **172721**); RNI [now PN] de Namoroka (FMNH 167563-167566; UADBA 16169); RNI [now PN] de Namoroka, 26 km NW Andranomavo, Forêt d'Ambovonomby, 200 m, 16°28.2'S, 45°20.9?E (FMNH **175909**, **175910**, 175911); RNI [now PN] de Namoroka, 31 km NW Andranomavo, Forêt de Mahabo, 100 m, 16°23.4'S, 45°20.9'E (FMNH **175912**, **175913**); RNI [now PN] de Namoroka, Site Andriabe, 2.0 km SE Namoroka (village), 16°24.4'S, 45°18.4'E, 110 m (FMNH 178587, 178591-178593).

Eliurus carletoni: Antsiranana Province: RS d'Ankarana, 2.6 km E Andrafiabe, forest near Andrafiabe Cave, 50 m, 12°55.9'S, 49°03.4'E (FMNH **169718**, **169719**, 169720); RS d'Ankarana, Campement des Anglais (Anilotra), 7.5 km NW Mahamasina, 125 m, 12°54.5'S, 49°06.6'E (FMNH **173104**, **173105**, **173106**, **173109**); RS d'Ankarana, 10 km NW Mahamasina, 100 m, 12°53.2'S, 49°06.6'E (FMNH **173107**, **173108**).

Eliurus danieli: Fianarantsoa Province: PN de l'Isalo, 28 km SE Berenty-Betsileo, along Sahanafa River near foot of Bevato Mountain, 22°19.0'S, 45°17.6'E, 650 m (FMNH 175934, UADBA **10483**); PN de l'Isalo, 24 km W Ranohira bas, Andranohavo (Canyon des Rats), 22°28.9'S, 45°22.9'E, 700 m (FMNH 175933).

Eliurus majori: Antsiranana Province: PN de Montagne d'Ambre, 12 km SW Joffreville, Grand Lac, 1325 m, 12°35.8'S, 49°09.6'E (FMNH 154345); PN de Montagne d'Ambre, 5.5 km SW Joffreville, 1000 m, 12°31.6'S, 49°10.3'E (FMNH 156341-156344, 154603-154609, **154610**, 154611-154616). Province de Fianarantsoa : PN de Midongy-Sud, NE slope Mt Papango, 3.5 km SW Befotaka, 1100–1450 m, 23°50.3'S, 46°57.5'E (FMNH **178686**).

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A tiny new species of *Sylvisorex* (Mammalia: Soricidae) from the Bamenda Highlands, Cameroon

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Abstract. A new species of shrew, *Sylvisorex silvanorum* n. sp., is described from specimens collected near Lake Bambili in the Bamenda Highlands of North West Cameroon. It is one of the smallest species of the genus occurring in the highlands of Cameroon and may be the sister taxon to *S. vulcanorum* from eastern Africa. Together with the rodents *Colomys eisentrauti* and *Lophuromys eisentrauti*, the new species forms a set of species currently known only from the Lake Bambili area.

Keywords. Africa, Cameroon, Lake Bambili, forest, shrew, *Sylvisorex*, new species.

1. INTRODUCTION

Shrews of the genus *Sylvisorex* Thomas, 1904 are restricted to lowland and montane forests of central Africa, from Cameroon/Nigeria in the northwest to Tanzania in the southeast. Currently 12 extant species are recognized (HUTTERER 2005), but recent fieldwork has yielded further species that will be described in the near future. Other species new to science still rest in museum collections and await formal description, such as the one named and described below. It was recognized as new by the senior author more than 30 years ago but known only from a single incomplete specimen since until additional material became available from owl pellets collected in 2003 by the junior authors which finally enabled us to define the new species.

2. MATERIAL AND METHODS

The holotype of the new taxon was collected during a Museum Koenig expedition to Cameroon from winter 1973 to spring 1974; see BÖHME (1975) for a brief description of the expedition. The participants W. BÖHME and W. HARTWIG visited the Bafut Ngemba Forest Reserve and the adjacent Bambili craters during March 1974. Shrews were collected with snap traps set along creeks and in undergrowth. The few shrews collected were briefly discussed by HEIM DE BALSAC (1975) but never properly documented.

Pellets of the African grass owl *Tyto capensis* were collected during November 2001 in the lower of the two Bambili volcano craters, about 8 km SE from Bamenda city, Bamenda Highlands, Cameroon (5° 55' N, 10° 14' E, 2 400 m a.s.l.) (RIEGERT et al. 2008). Both volcano calderas were flooded by lakes in the past (ANONYMOUS 1972). The lake persists only in the lower crater, the upper one has been gradually covered by wet grasslands.

Skull measurements were taken with an electronic calliper. All measurements are given in millimetres (mm), and body mass in grams (g). The terminology of cranial and dental structures follows MEESTER (1963) and JENKINS (1984); external and cranial measurements are the same as previously defined by STANLEY et al. (2005) and KERBIS PETERHANS et al. (2008). Voucher specimens mentioned in the text are deposited in the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK) and in The Natural History Museum, London (BMNH). The taxonomy follows HUTTERER (2005).

3. THE NEW AFRICAN PYGMY SHREW

Sylvisorex silvanorum n. sp.

Holotype and type locality. Skin and partial skull of a young adult female (ZFMK 74.430), collected by W.

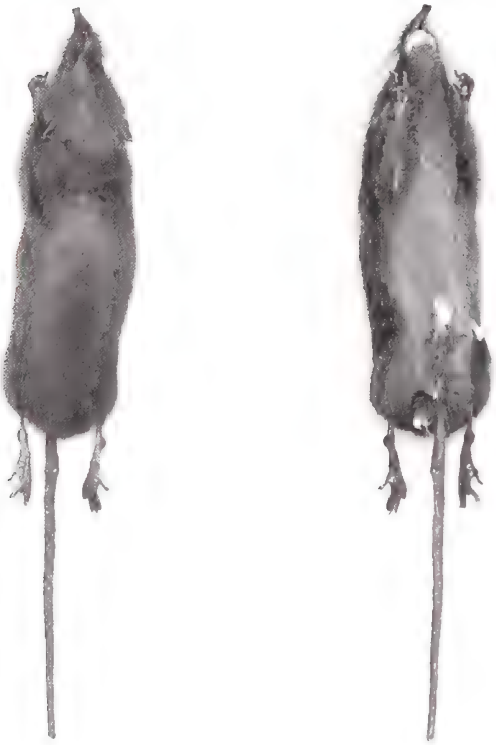

Fig. 1. *Sylvisorex silvanorum* n. sp., skin of holotype (ZFMK 74.430) in dorsal and ventral view. Total length is 99 mm.

Böhme and W. Hartwig on 07.03.1974 (field no. 98) near Lake Bambili, Mt. Lefo, Bafut Ngemba F. R. (5° 55' N, 10° 14' E), 1 800–1 900 m a.s.l., Bamenda Highlands, North West Province, Cameroon.

Measurements of holotype. Head and body length 52 mm, tail 44 mm, hind foot length 11.5 mm, ear conch 5.0 mm.

Paratypes. Two incomplete skulls (ZFMK 2003.1103, 2003.1104) removed from pellets of *Tyto capensis*, collected November 2001 by J. Riegert and O. Sedláček on a slope of the lower Bambili volcano craters (5° 55' N, 10° 14' E, 2 400 m a.s.l.), about 8 km SE of the city of Bamenda, Bamenda Highlands, NW Province, Camty of Bamenda, Bamenda Highlands, NW Province, Cameroon (Riegert et al. 2008).

Diagnosis. A very small and dark species of *Sylvisorex* with a total length below 100 mm, tail 85 % of head and body length; no long bristle hairs on tail.

Description. *Sylvisorex silvanorum* n. sp. is a small terrestrial shrew with dark fur. The hairs on the dorsum are dark brown, between Fuscous (Ridgway 1912, plate XLVI) and Chaetura Drab. Ventrally the hairs gradually turn into Hair Brown. Hairs on dorsum are about 3.4 mm in length; ventrally they are slightly shorter. The basal portion of individual hairs is Dark Plumbeous (Plate LII) with tips Drab to Hair Brown (Plate XLVI). The entire body, including head, ears, limbs, and tail have the same dark colour, only the central part of the belly is a bit lighter (Fig. 1). Facial vibrissae reach 14 mm in length. Ear conch is small, round and pocketed, and covered by very short hairs, except for the inner fold which carries a row of long hairs. Hind foot narrow, with elongate digits and short claws. Ventral inner surface of hind foot covered by small granule-like bumps, heel covered by short hairs. Tail of medium length (85% of head and body length); colour uniform, no long bristle hairs present.

Table 1. External measurements of S*ylvisorex silvanorum* and other small species of the genus with no long bristle hairs on the tail.

Species	TL	HB	Tail	HF	Ear	Wt	Tail/HB
S. johnstoni[1]	64	39	25	9	–	–	64%
S. silvanorum[1]	99	55	44	10.0	4.8	–	85%
S. vulcanorum[2]	95.9	49	46.9	10.4	6.4	3.5	96%
S. camerunensis[1]	122	65	57	12	9	5	87.6%
S. granti[2]	114	58	55.9	11.6	7.5	–	96.4%
S. isabellae[1]	119	60	59	13	6	8	98.3%
S. morio[3]	119	71	51	13	10	8	72%

[1] holotype; [2] means of measurements taken from Hutterer & Verheyen (1985); [3] ZFMK 69.370.

Skull (Figs. 2, 3) short with a rounded braincase. Dorsal profile (Fig. 3) inflated, rostrum short but slender. Interorbital constriction relatively broad (24.9% of estimated condylo-incisive length). Infra-orbital bridge narrow, lachrymal foramen large.

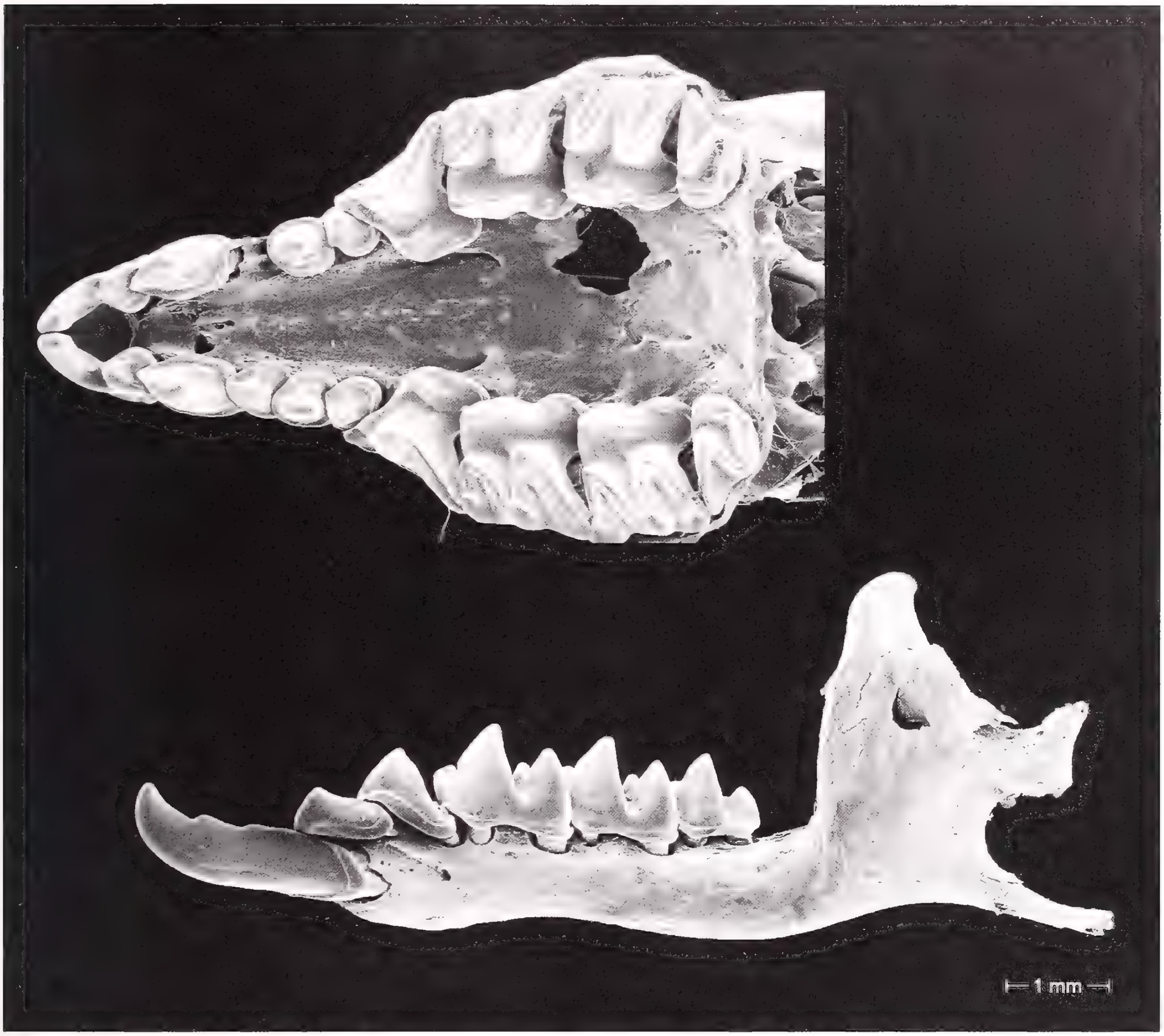

Fig. 2. *Sylvisorex silvanorum* n. sp., skull of holotype; cranium and upper dentition in occlusal view, and left mandible in labial view. Scale 1 mm.

Upper teeth: First upper incisor small, with a sharp anterior tip and a well-developed talon. First upper unicuspid large, second and third unicuspids half and fourth unicuspid a quarter of the length of the first unicuspid. P4 with a small parastyle and a large paracone; the protocone is well expressed. M1-2 square-shaped in occlusal view, protocone strongly developed. M3 relatively large (0.69 x 1.14 mm in the holotype).

Mandible: Slender with thin ramus and weak coronoid process. Foramen mentale below posterior root of lower p4. Condyle small, oblique, and about as wide as high.

Lower teeth: Tip of first incisor curved upwards, with two denticulations on cutting blade. Lower p4 as long as wide (occlusal view). Lower molars long and slender; third lower molar (1.11 x 0.54 mm) with a deep talonid basin.

Comparisons. The species is not easily recognized in the field. Heim de Balsac (1975) identified all three specimens of *Sylvisorex* collected in 1974 near the Bambili crater as belonging to "*Sylvisorex granti* Thomas, 1907", but a subsequent inspection of the same material by the senior author revealed that one (field no. 98) represented the new *S. silvanorum*, another (field no. 106) *S. camerunensis*, and a third (field no. 113) a new species (not yet described) related to *S. morio*, a species restricted to Mount Cameroon. *S. silvanorum* is smaller in external and cranial measurements (Tables 1, 2) than most other species of *Sylvisorex*, with the exception of *S. john-*

Table 2. Cranio-dental measurements of *Sylvisorex silvanorum* and allies.

Species	CI	PL	UTR	IO	MB	GW	PGL	HCC	LTR	COR
S. johnstoni[1]	15.0	6.1	6.4	3.8	4.7	7.1	-	3.8	5.9	3.5
S. silvanorum[2]	-	5.80	6.36	3.99	4.61	-	-	-	5.92	3.45
S. silvanorum[3]	c.15.6	5.90	6.72	3.82	5.13	7.94	5.57	5.20	-	-
S. silvanorum[4]	-	-	7.20	3.83	-	-	-	-	5.80	3.74
S. vulcanorum[5]	15.8	5.90	6.6	4.0	5.0	7.8	5.28	4.90	6.1	3.6
S. camerunensis[6]	17.14	6.85	7.46	4.12	5.13	8.50	5.75	4.77	6.81	3.89
S. granti[7]	16.60	6.68	7.19	3.99	5.28	8.12	5.42	4.41	6.48	3.96
S. isabellae[8]	18.81	7.55	8.14	4.43	5.72	9.30	6.08	5.41	7.48	4.42
S. morio[9]	19.63	8.22	8.55	4.50	5.56	9.38	6.22	5.44	7.87	4.30

[1] holotype BMNH 87.11.26.1; [2] holotype ZFMK 74.430; [3] paratype ZFMK 2003.1103; [4] paratype ZFMK 2003.1104; [5] average measurements of type series (n=6) from HUTTERER & VERHEYEN (1985); [6] holotype ZFMK 69.358; [7] ZFMK 68.538; [8] holotype ZFMK 69.365; [9] ZFMK 69.370; all measurements taken by RH.

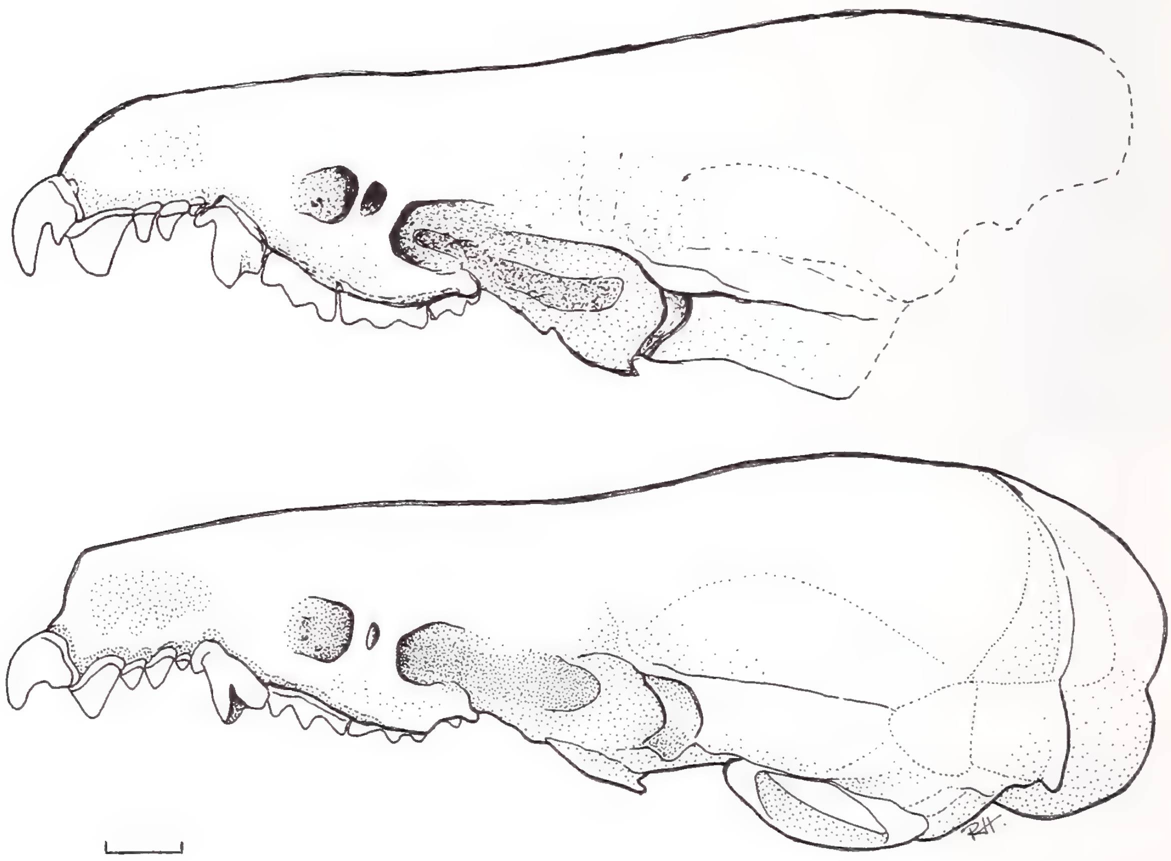

Fig. 3. *Sylvisorex silvanorum* n. sp. (upper figure, combined drawing taken from holotype and paratype), lateral view of the skull compared to *Sylvisorex vulcanorum* (lower figure, holotype from HUTTERER & VERHEYEN 1985); scale 1 mm.

Table 3. Species of small mammals recorded from the Bambili area in 1974 and 2001.

Species	1974* Traps, shotgun	2001** *Tyto capensis*	2001** *Bubo cinerascens*	Species endemic to Bamenda Highlands	Species endemic to Cameroon Mountains
Sylvisorex silvanorum n. sp.	1	2		X	X
Sylvisorex cf. *morio*	1			X	X
Sylvisorex camerunensis	1	16	2	X	X
Myosorex okuensis	3	10	3	X	X
Crocidura olivieri	1	2	1		
Crocidura virgata		5			
Crocidura attila			1		
Paraxerus cooperi	11				X
Graphiurus lorraineus	6				
Lophuromys eisentrauti	2			X	X
Lophuromys sikapusi			1		
Hybomys eisentrauti	4			X	X
Colomys eisentrauti	3			X	X
Dasymys rufulus		1	9		
Hylomyscus aeta	1				
Lemniscomys striatus		2	1		
Praomys hartwigi	1	2	2	X	X
Otomys occidentalis		3	5		X
Mastomys sp.		10	4		
Mus musculoides		1	4		
Mus setulosus		4			
Muridae indet.		5			
Totals	35	63	33	8	10

* Heim de Balsac (1975), Dieterlen (1979, 1983), Hutterer et al. (1992), Van der Straeten & Hutterer (1984), Hutterer (unpublished); ** Riegert et al. (2008).

stoni (Dobson, 1888). The latter has a much shorter tail, shorter hind feet, and a shorter skull (Hutterer & Verheyen 1985). There is only one species which is similar in size and form: *Sylvisorex vulcanorum* Hutterer & Verheyen, 1985, a species known only from high elevations (1900–3000 m) of the Albertine Rift, separated from the Bamenda Highlands by some 2000 km of lowland forest and savannah. *S. silvanorum* n. sp. differs from *S. vulcanorum* by a shorter tail (44 versus 46.9 mm), and by cranial details. In *S. silvanorum* n. sp., the lachrymal foramen is large (small in *S. vulcanorum*), the first upper incisor is pointed (short and rounded in *S. vulcanorum*), and the second and third upper unicuspids are about equal in size (second smaller than third in *S. vulcanorum*). The few available measurements may also indicate that the upper tooth row is slightly shorter in *S. vulcanorum*. It is probable that both species represent sister taxa, a hypothesis which will have to be tested with genetic data in the future.

Some other small species of *Sylvisorex*, such as *S. konganensis* Ray & Hutterer, 1996, *S. pluvialis* Hutterer & Schlitter, 1996, or *S. akaibei* Mukinzi, Hutterer & Barriere, 2009, were not considered because they are easily distinguished, even in the field, by their hairy tails; they also have very different skulls (Ray & Hutterer 1996, Hutterer & Schlitter 1996, Mukinzi et al. 2009). Small and dark-furred species of *Suncus* which occur in Central African lowland and mountain forest, e.g. *S. infinitesimus* (Heller, 1912), *S. remyi* Brosset, Dubost & Heim de Balsac, 1965, *S. hututsi* Kerbis Peterhans & Hutterer, 2009, are all smaller in external and cranial dimensions, and have shorter tails covered with long and numerous bristle hairs (Kerbis Peterhans & Hutterer 2009).

Habitat. The holotype specimen was collected in dense undergrowth along a stream running down from the relict montane forest of the reserve towards the Bambili crater

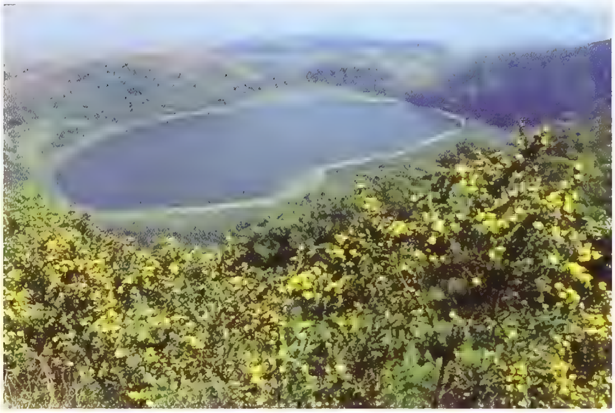

Fig. 4. Lower Bambili crater showing relict montane forest on the slopes and montane grassland along the shore of the lake. Photograph taken in 2001.

(W. BÖHME, field notes). The slopes of the lower Bambili crater are covered by a mosaic of montane forest, *Lasiosiphon* and bamboo woods and grassland. The slopes are partly rocky (Fig. 4). The surroundings of the craters are covered mainly by extensive pastures, *Pteridium* fern growth and open *Lasiosiphon* woods. It is not known where the owls picked up the shrews but the slope forest and the wet grassland bordering the lake may constitute suitable habitats.

Etymology. Derived from *silvanus* (Latin, meaning forest god). We dedicate this cryptic pygmy shrew to the sylvans, small and invisible forest creatures occurring in the beliefs, mythologies, and fairy tales of Africans, Europeans, and many other peoples on earth. As a common name we suggest "Bamenda pygmy shrew".

DISCUSSION

The forests around Mt. Lefo are still full of mysteries. During their field work in 1974, BÖHME and HARTWIG collected 35 specimens, representing 12 species of shrews and rodents (Table 3). Four of the species were subsequently described as new taxa: *Colomys* (*goslingi*) *eisentrauti* Dieterlen, 1983, *Lophuromys (sikapusi) eisentrauti* Dieterlen, 1979, *Hybomys eisentrauti* Van der Straeten & Hutterer, 1986 (tentatively assigned to *Hybomys* cf. *badius* by MUSSER & CARLETON 2005), and *Sylvisorex silvanorum* n. sp. (see DIETERLEN 1979, 1983, VAN DER STRAETEN & HUTTERER 1986). A further species of *Sylvisorex* still awaits description. HUTTERER et al. (1992) proposed full species rank for *Lophuromys eisentrauti*, and further but yet unpublished research suggests that *Colomys eisentrauti* and *Hybomys eisentrauti* may deserve species status as well. The forests around Mount Lefo (including the Bambili craters) apparently house a number of local endemic mammals, some of which may be threatened with extinction. The local *Colomys eisentrauti* and *Lophuromys eisentrauti* have not been found again since their discovery in 1974. At least four mammal species are only known from the Lefo Mountains, 8 from the Bamenda Plateau, and more than 10 are endemic to the Cameroon Mountains chain (HUTTERER et al. 1992). STAGER & ANFANG-SUTTER (1999) provided evidence from lake sediment cores of pronounced climatic changes in the West Cameroon Highlands since 24,000 years BP, particularly in the Lake Bambili area. It is probable that such climatic fluctuations triggered speciation in the Bambili area and other highlands in NW Cameroon (EISENTRAUT 1973).

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Zusammenfassung. Eine neue Spitzmausart, *Sylvisorex silvanorum* n. sp., wird nach Material, das am Bambili-Kratersee im Bamenda Hochland Nordwest-Kameruns gesammelt wurde, beschrieben. Es handelt sich um eine der kleinsten Arten der Gattung, die vermutlich die Schwesterart zu *S. vulcanorum* aus Ostafrika ist. Wie die Nagerarten *Colomys eisentrauti* und *Lophuromys eisentrauti* ist die neue *Sylvisorex*-Art bisher nur aus der Umgebung des Bambili-Kraters bekannt.

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Altitudinal distribution and anthropogenic influence on small mammal assemblages on Mount Kupe, SW Cameroon

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Abstract. We conducted a taxonomical inventory of small mammal biodiversity on Mount Kupe, SW Cameroon, the second inventory on that mountain after M. Eisentraut's more than 50 years ago. Our survey yielded a total catch of 19 species of mammals: 16 rodents, two bats, and one shrew. For each species we summarize data on natural history and discuss taxonomical and distributional aspects. We observed a difference between the rodent assemblages of the lowland (below 1000 m) (including *Praomys misonnei*) and the upper sub-montane and montane forest (1500–2000 m) (including *Hylomyscus* cf. *walterverheyeni*, identified for the first time from the Cameroon Mountains). This seems to correspond to previously described vegetation changes between 1000 and 1500 m. The inhabited and cultivated zones at the base of Mt. Kupe yielded eight widely-distributed rodent species. A number of taxonomical problems concerning montane forest species remain to be solved.

Keywords. Africa, Cameroon, Chiroptera, Rodentia, Soricomorpha, taxonomy, diversity.

1. INTRODUCTION

Tropical regions are well known to have a higher biodiversity than temperate regions. The forests of west-central Africa have been described as one of the tropical "hot spots" (Myers et al. 2000; Kuper et al. 2005). African mountains seem to harbour a very important endemic diversity and are of exceptional conservation importance (Heim de Balsac 1968; Eisentraut 1973; Gentry 1992; Stanley et al. 1998, 2005; Kasangaki et al. 2003; Herrmann et al. 2005; Burgess et al. 2007). Both lowland and mountain forests are presently subject to intense deforestation. Several authors have emphasized the role of African forest refugia in promoting speciation during Quaternary climatic changes (Maley 1987, 1996; Querouil et al. 2003, Plana et al. 2004; Behnin 2006, Huhndorf et al. 2007). However, the knowledge of the mechanisms by which so many species arise and differentiate in such regions depends directly on a precise characterization of their biodiversity in relation to altitudinal and vegetation shifts along elevational gradients. The altitudinal effect on small mammal diversity is not well known and available studies differ in their results. According to some authors species-richness is not uniformly distributed on mountains, but the base and the top hold a higher diversity than the intermediate zones (Brown 2001; Lomolino 2001). Other authors found a continuous decrease of diversity with elevation (Diaz et al. 2002; Kasangaki et al. 2003) or contrasting patterns in different taxonomic groups (Hofer et al. 2000). However, a positive correlation between species turnover and elevation was recently evidenced for rodents of different tropical mountains (Mena & Vasquez-Dominguez 2005). The authors considered climate, productivity and landscape heterogeneity as well as historical factors as possible explanations for elevational gradients.

There are many other vertebrate groups for which zonation has been described as a function of altitude in African mountains (e.g. Eisentraut 1968; Amiet 1987; Stuart et al. 1987; Kityo & Clausnitzer 2001; Kasangaki et al. 2003) but the observed changes seem to vary locally and their causes are not well understood. It is well known that the composition of plant communities changes along altitudinal gradients but the respective roles of vegetation or available streams versus altitudinal change remain unclear (Hofer et al. 2000). Because most terrestrial small mammal species are primary consumers or have limited dispersal capacities (restricted ranges and/or habitats) they are good models for studying altitude-diversity gradients.

Situated in the Central African forests blocks of the Guineo-Congolese hot spot of biodiversity and extending for about 1600 km, the Cameroon Volcanic Line (CVL) is a succession of high volcanoes and plateaus ranging in age between 30 and one Myr (Ubangoh et al. 1998). At a distance of about 3000 km from the Western Rift Valley of East Africa, it represents the second highest range of mountains in Africa, with Mount Cameroon at 4100 m and Mount Oku at 3011 m. Because of difficult access the Cameroon Highlands ecoregion has been poorly sampled for its small mammal fauna. Small mammal expeditions were launched by Eisentraut (1957, 1961, 1963, 1968), Lamotte (1950–1970, unpublished), and Schlitter et al. (1999), among others. These studies showed a high endemism of the region, particularly in Afro-alpine grasslands (above 2000–2500 m) and in mountain forests (Eisentraut 1963; Heim de Balsac 1968; Lamotte & Petter 1981; Petter 1986; Dieterlen & Van der Straeten 1992; Hutterer et al. 1992; Verheyen et al. 1997). Studies on other vertebrates and plants have also described many endemics, emphasizing the importance of this region (Stuart 1986; Amiet 1987; Sosef 1994; Larison et al. 2000; Cheek et al. 2004; Herrmann et al. 2005). Most previous biodiversity inventories focused on the two highest mountains (i.e. Mount Cameroon and Mount Oku). The biodiversity of the other mountains in the region is poorly known (summarized by Hutterer et al. 1992). Among the CVL highlands, Kupe Mountain (2064 m) harbours a well preserved mountain forest in the Bakossi Highlands. This forest is conserved on the western side of the mountain, thanks to the Bakossi people and a nature reserve project monitored by the World Wildlife Fund (WWF). While its vegetation has been extensively studied (Cheek et al. 2004; Tchiengue 2004), its small mammal diversity is less well known; Eisentraut (1958, 1963) published a faunal list for this mountain. Mt. Kupe is famous for the presence of ten primate species, among them drill (*Mandrillus leucophaeus*) and chimpanzee (*Pan troglodytes)* populations, which are threatened with extinction (Wild et al. 2004, 2005). The forest elephant (*Loxodonta africana cyclotis)* is also present on Mt. Kupe (Wild 2004). Numerous woody plant species of the lowland forest exhibit distinct sub–montane forest 'forms' (Letouzey 1985). Most of them still have no taxonomic status and were not included in assessments of diversity, endemism and the impacts of ecological change. Several studies (e.g. Breteler 1999; Mc Key 2000) have demonstrated the distinctness of sub-montane forest species, as well as their key role in understanding the history of the lineages concerned.

With this information as a background we concentrated our small mammal survey on the montane and sub-montane species. Our study should be of conservation value and provide further biogeographical hypotheses. In this paper we describe the composition of the small mammal community of Mt. Kupe along an altitudinal gradient. In order to better describe the Mt. Kupe small mammal community we made a morphological and molecular inventory of small mammal species to accurately describe the degree of endemism of the Kupe fauna, and eventually also look at a possible altitudinal difference between submontane and montane communities. This should further allow us to evaluate the importance of the CVL for small mammal biodiversity conservation and diversification.

1.1. Background

Previous information on the Mt. Kupe small mammal fauna: Small mammals from the Cameroon Volcanic Line (CVL) were described by Sanderson (1940) and Eisentraut (1957, 1961, 1963, 1968, 1969). They mainly studied the small mammals from Mt. Cameroon and Bioko Island, but also collected specimens from the massif of Mt. Kupe. M. Lamotte's surveys (1970–1975) followed and his collections allowed the description and rehabilitation of endemic species in the Bamenda Highlands (Lamotte & Petter 1981; Petter 1986; Musser & Carleton 2005), but not the Bakossi Highlands. In an unpublished report Dowsett-Lemaire & Dowsett (1998) provided a faunal list of the Bakossi Mountains. This list contained a great number of unidentified species.

The study area: Mt. Kupe is situated on the western slopes of the CVL. It is a steep-sided massive horst block formed during Cameroon's third eruptive phase in the Quaternary (Wild 2004). Mt. Kupe is the youngest mountain of the Bakossi Highlands. The mountains of this highland are among the wettest areas in Africa (around six to seven metres annual rainfall, Cheek et al. 2004). Approximately 80 % of it occurs in the April-October wet season but in general every month of the year experiences rainfall. Nevertheless, there is a dry season between November and March, and a single week or two of bright sunshine without rain usually occurs in July (the "short dry season"). Humidity is exceptionally high. The minimum relative humidity (81 %) is recorded during the dry season.

Descriptions of the Kupe forest vary from one author to another. All authors agree that the lowland evergreen forest occurs between 150 to 800 m and is restricted to the western and southern part of Mt. Kupe. The sub-montane forest is found from 800 m asl to the summit; Cheek et al. (2004) consider it to be constituted by mid-altitude forest and Afro-montane rain forest. Previously, Thomas

(1986) recognized only two forest types: the lowland forest below 1600 m and the sub-montane forest above. This classification is not followed by LANE (1994) or by CHEEK et al. (2004). The sub-montane forest is characterized by the presence of *Podocarpus milanjianus* (Podocarpaceae) around 1600–2000 m, *Santiria trimera* (Burseraceae) and numerous large Guttiferae (Clusiaceae) of the genera *Allanblackia, Pentadesma*, and *Symphonia* between 1000 m and 2000 m, and *Cola* (Sterculiaceae) also between 1000 m and 2000 m (LETOUZEY 1968). LETOUZEY (1968) divides the sub-montane forest into three blocks. According to CHEEK et al. (2004) this point of view was based mainly on aerial observation and it is possible that the band of vegetation influenced by human activity in this area was misinterpreted as sub-montane thicket. CHEEK et al. (2004) divided the sub-montane forest into two altitudinal types: the lower sub-montane forest (800–1400 m), harbouring a high epiphyte and saprophyte diversity with some of the Bakossi Highlands endemics, and the upper sub-montane forest (1400–1900 m) which is less diverse. According to CHEEK et al. (2004) there is also a montane forest (from 1900 m to the summit), characterized by the absence of *Clausena anisata*, *Laesa lanceolata*, and *Pavetta hookeriana*, all otherwise frequent in montane forests of the Cameroon Highlands. On the other hand, it contains many endemic species such as *Leptoderris fasciaculata*, *Batesanthus purpureus* (also sub-montane), *Ficus oreodryadum*, *Zanthoxylum leprieurii*, and *Aframomum zambeziacum*. A patch of mountain grassland is found on each of the three peaks of the summit which are up to 100 m wide only (CHEEK et al. 2004). These mountain grasslands are constituted by two species only: *Panicum hochstetteri* and *Gladiolus aequinoctialis*.

2. MATERIALS AND METHODS

Small mammals were trapped during three periods of fieldwork. December 2005: around Nyasoso (N 04° 50' / E 09° 40') and on the mountain below at 950 m; February 2006: between 1500 m and 2000 m; August 2006: around 1000 m (Table 1). Lines of 250 Sherman traps baited with peanuts, flour, oil and dry fish were used each time and were set in six habitats: cultivated lowland and secondary forest (100–800 m), lower sub-montane forest (900–1000 m), upper sub-montane forest (1500 m), montane forest and montane grassland (2000 m). The traps were checked twice per day. Additionally, a number of traditional traps set by hunters were put randomly in the surroundings of Nyasoso village and at the summit. We also put two mist nets at the entrance of a cave (900 m asl) during two nights in December 2005 in order to catch Chiroptera. Due to logistic constraints the number of trap nights varied between habitats. Standard external measurements (weight [W], head and body length [HB], tail length [TL], ear [E] and hindfoot lengths [HF]) and the sex of each animal were taken. All animals were autopsied. The liver was kept in 70 % ethanol for molecular identifications and the carcasses preserved in 4 % formalin, and the skulls cleaned. All this material was included in the MNHN collections, Paris. Comparisons were performed with specimens previously collected from Cameroon (Nditam and Dja regions), Gabon (Makokou, Belinga) and Central African Republic (La Maboké). All species were identified based on information published in ROSEVEAR (1969), VIVIEN (1991) and WILSON & REEDER (2005).

For species identification we performed classical morphometric analysis on both external and cranial distances, using a digital caliper (MITUYOTO, precision 0,01mm) and the protocol described by DENYS & TRANIER (1992). Due to the abundance of sibling species in tropical Africa, 81 specimens were sequenced by one of us (ADM) for confirmation of identification (Cytochrome b and/or 16S genes). These specimens were compared using the Neighbour Joining Tree Analysis and the sequences available in Genbank.

To study the small mammal communities, we used the Shannon-Wiener diversity index $H = -\sum_{i=1}^{s} p_i \ln p_i$ as a direct measure of species diversity in each habitat, as well as a correspondence analysis on presence-absence data. The correspondence analysis CFA (BENZECRI & BENZECRI 1984) was performed on the presence-absence of species in different habitats. By reducing the number of variables and using the chi-square distance, this method allows the representation of the relationship between variables (here habitats) and individuals (here species) on the same graph (scatter plot type) and gives an overview of the distribution of species diversity. All statistical analyses were performed by using XLSTAT 7.1 software (Addinsoft).

3. RESULTS

3.1. Trapping success, faunal lists

In total, 98 small mammals belonging to 19 species were captured on Mt. Kupe. Overall trap success with Sherman traps was 3,03 %. This varied among habitats: trap success was always low in the forest, varying from 1,86 % to 2,88 %, depending on the altitude; it was higher in habitats under anthropogenic influence (5,51 %; Table 2). The Shannon diversity index indicates quite an equal distribution of species abundances in the habitats under anthropogenic influence and the low diversity of the sub-montane and montane forests.

Table 1. Characteristics of the different habitats investigated and periods when they were sampled.

Sampling period	Elevation range (m)	Main vegetation investigated	Main habitats	GPS coordinates	Collecting method
Dec 2004 beginning of dry season	850	anthropogenic	farmland	–	Traditional traps
		lowland forest	closed canopy	–	Traditional traps
		anthropogenic lines A,B,C,F	fallow, farmland	N 04° 50’ 10,1”/ E 09° 40’ 48,5”	Sherman traps (60)
Dec 2005 beginning of dry season	850–950	anthropogenic	home garden	N 04° 50’ 09,6”/ E 09° 40’ 51,2”	Sherman traps (40)
		lowland forest lines D,E,T,U,V	closed canopy	N 04° 49’ 26,0”/ E 09° 41’ 11,9”	Sherman traps (160)
	850	anthropogenic line C	fallow, farmland, home garden	N 04° 50’ / E 09° 40’	Sherman traps (100)
Febr 2006 end of dry season	1500–1600	sub-montane forest lines O,P,Q,R,S	closed canopy, dense under story	N 04° 49’ 08,7”/ E 09° 42’ 27,1”	Sherman traps (250)
	1900–2000	montane forest lines K,L,M	closed canopy	N 04° 47’ 51,1”/ E 09° 42’ 11,2”	Sherman (250) and traditional traps
		montane grassland lines I,J	woodland, savannah	N 04° 47’ 52,7”/ E 09° 42’ 23,9”	Sherman traps (250)
August 2006 little dry season	850	lowland forest	closed canopy	N 04° 49’ 26,0”/ E 09° 41’ 11,9”	Sherman traps (250)

Table 2. Details of trapping efforts and success in each habitat sampled. The trapping success corresponds only to animals captured in Sherman traps and the Shannon Index was calculated on pooled Sherman + Traditional trap captures in all habitats.

Species/Trap success/Diversity/H’	**Anthropogenic**		**Lowland forest**		**Sub-montane forest**		**Montane forest 2000m**	
	Sher	Trad	Sher	Trad	Sher	Trad	Sher	Trad
Crocidura poensis complex	4	0	1	0	0	0	0	0
Cricetomys cf. *emini*	0	1	0	0	0	0	0	3
Dendromus sp.	0	1	0	0	0	0	0	0
Deomys ferrugineus	0	0	0	0	2	0	0	0
Grammomys poensis	2	1	0	0	0	0	0	0
Hybomys cf. *univittatus*	0	0	1	0	0	0	0	0
Hylomyscus walterverheyeni	0	0	10	0	12	0	12	0
Hylomyscus sp.	0	0	1	0	0	0	0	0
Lemniscomys striatus	2	0	0	0	0	0	0	0
Lophuromys cf. *sikapusi*	0	3	0	0	0	0	0	0
Malacomys longipes	0	0	3	0	0	0	0	0
Mastomys natalensis	1	0	0	0	0	0	0	0
Mus musculus	0	2	0	0	0	0	0	0
Mus setulosus	4	1	1	0	0	0	0	0
Oenomys hypoxanthus	8	3	0	0	0	0	0	0
Praomys jacksoni	2	1	0	0	0	0	0	0
Praomys misonnei	0	0	13	0	0	0	0	0
Sherman trap nights	471	-	1041	–	751	–	637	–
Sherman captures	23	13	30	0	14	0	12	3
Trap success per night (%)	**5.51**	–	**2.88**	–	**1.86**	–	**1.88**	–
Diversity	**7**	**8**	**7**	**0**	**2**	**0**	**1**	**1**
H’ (pooled Sher+Trad/habitat)	**0,921**		**0,456**		**0,178**		**0,217**	

Table 3. Means and ranges for the standard external measurements [mm] of the Mt. Kupe rodents.

Measurements	HB	TL	HF	E
Oenomys hypoxanthus (n=11)	149 (110–168,5)	177,3 (151–194)	31 (23–36)	18 (13–20)
Malacomys longipes (n=3)	137,7 (130–142)	161 (151–167)	35,3 (32–35)	20,3 (20–21)
Lemniscomys striatus (n=2)	109–122	111–115	25–26	15–16
Mus setulosus (n=5)	74,9 (63,5–84)	53,5 (50–57,5)	14,8 (14–16)	11,7 (10,5–14)
Hybomys cf. *univitatus* (n=1)	160	93	28	15
Grammomys poensis (n=3)	122 (116–133)	178,7 (171–189)	25 (21–28)	15,3 (15–16)
Hylomyscus walterverheyenei (n=28)	89,2 (74–103)	129,34 (112–150)	18,22 (12–21)	14,56 (13–16)
Hylomyscus sp. (n=1)	73	112	19	16
Praomys jacksoni (n=3)	120,3 (100–132)	125 (113–139)	24,3 (24–25)	18 (16–19)
Praomys misonnei (n=10)	117,9 (100–197)	133 (115–160)	23,65 (21,5–28)	17,25 (15,5–19)
Dendromus sp.(n=1)	55	84	19	10
Cricetomys emini (n=3)	347,7 (340–358)	371 (350–391)	66 (65–67)	39,7 (39–40)
Lophuromys cf. *sikapusi* (n=2)	130–142	59–70	20	17
Deomys ferrugineus (n=2)	119–137	172–191,5	33–36	25
Mastomys natalensis (n=1)	113,5	112	20	17

In total, 16 rodent species were captured. The most abundant species was *Hylomyscus walterverheyeni* (35, 80 % of captures), followed by *Praomys misonnei* (13,68 %) and *Oenomys hypoxanthus* (11,58 %). Only one shrew species (*Crocidura* cf. *poensis*) and two bat species (*Epomops franqueti* and *Myonycteris torquata*) were captured. The maximum diversity was found in the habitats under anthropogenic influence and in lowland forest. Eight species were trapped in the former habitat type, with *Oenomys hypoxanthus* and *Mus setulosus* being the most abundant. The absence of *Hylomyscus* cf. *walterverheyeni* from this habitat type is noteworthy, compared to its general abundance in the natural types. In the lowland forest *Hylomyscus walterverheyeni* and *Praomys misonnei* dominate the assemblages. The montane grassland yielded no captures. The sub-montane and the montane forest habitats' diversity are low with two species each and are characterized both by the presence of *Hylomycus walterveheyeni*.

3.2. Species records, characteristics and systematic notes

In this species account we provide morphological and/or habitat characteristics for each species. Where confusion with another species is possible we also provide results from skull analysis and cyt b or 16S DNA sequences analysis.

Order Rodentia

Family Muridae Illiger, 1811

Oenomys hypoxanthus Pucheran, 1855

Six males and five females (one juvenile) of this species were recorded. Standard measurements are provided in Table 3. Our specimens displayed the characteristic red nose of the genus and an underside of white-orange colors ventrally, with a more intense orange-red part in the genital region. The back fur displays a mixture of long black guard and short red-yellow hairs. The tail is covered with small black scales and is naked except for a few scattered, very short hairs. The Kupe specimens fall within the size range of specimens from Mount Cameroon (EISENTRAUT 1963) and S Nigeria (HAPPOLD 1987). *Oenomys hypoxanthus* shows appreciable geographic variation in fur color and body size; in Cameroon it was also captured in Nyasoso, Buea, Musake, Malende and Mueli (11 specimens) (EISENTRAUT 1963). During this inventory of the Mt. Kupe small mammal fauna, this species was only trapped at low altitude in Nyasoso village and in a fallow area with *Ageratum* spp. These results are congruent with the observations of KINGDON (1997) and HAPPOLD (1987), according to which *O. hypoxanthus* commonly nests in fallow ground and village gardens. It is generally restricted to forest below 2000 m.

Malacomys longipes Milne-Edwards, 1877

Three specimens (two males and one sub-adult female) were trapped in the forest along a river at an altitude of 850 m. They have a hindfoot longer than 34 mm (Table 3). The specimens from Nyasoso have a shorter ear (20–21mm) than those from Efulan (Cameroon) or Makokou/Belinga (Gabon) (25 mm), and their skull and body sizes are also smaller. These observed differences may have been a result of the low sample size of specimens captured from Nyasoso. Musser & Carleton (2005) recognized the existence of three species within the genus *Malacomys*, among which only *M. longipes* is mentioned in Central and South Cameroon. However, *M. longipes* and *M. edwardsi* occur both in South Nigeria (Happold 1987). Eisentraut (1963) found only seven specimens of *M. longipes* in Batoki, Malende and Isobi (Cameroon) and only one on Mt. Kupe at 900 m, but mentioned a great variety of pelage colours in his sample. Similarly Happold (1987) also mentioned that Cameroon specimens of *longipes* show considerable variation, and some individuals are almost the size of the smaller *edwardsi*. However, the comparison of our cyt b sequences to those available in Genbank allows the definite identification of the three specimens as *M. longipes*.

Lemniscomys striatus Linnaeus, 1758

Two male striped rats were trapped in a maize field at Nyasoso village, 800 m asl. They fall within the size variability and color of *L. striatus* from Central African Republic (CAR), Congo and Cameroon and have molecular affinities with representatives from the region (Nicolas et al. 2008a). A few earlier specimens had been collected in Nyasoso, Mt. Manengouba (Eisentraut 1973) and the Mamfe region (Sanderson 1940).

Mus (Nannomys) setulosus Peters, 1876

Eisentraut (1957) attributed the Nyasoso *Mus* specimens to *M. musculoides*, but mentioned that they have a browner pelage than specimens from Buea and Mt. Cameroon. Later, Eisentraut (1968) corrected the identification and attributed the *M. musculoides* specimens to *M. setulosus*, which we confirm here on morphological and molecular grounds. The type specimen of *M. setulosus* comes from Limbe (formerly Victoria), less than 100 km S of Mt. Kupe. We obtained six pygmy mice (two males and four females) attributed to *Mus* (*Nannomys) setulosus*, based on their dark pelage, rather large size (Table 3), and the presence of a second lobe on the lower M3 (Kouassi et al. 2008). They have been molecularly typed to confirm the identification (Kouassi et al. 2008); TL is somewhat shorter than HB. All six specimens were trapped in zones influenced by human activities and in lowland forest. One subadult female had 2+2 mammae, the other female was a juvenile.

Mus musculus Linnaeus, 1758

Two *M. musculus* males were trapped by inhabitants in Nyasoso village. Cyt b analysis confirmed their identification.

Hybomys cf. *univittatus* (Peters, 1876)

One sub-adult male was recorded in lowland forest. Both skull morphology and cyt b analyses identified it as *Hybomys* (Table 4). Eisentraut (1968, 1973) described only *H. univittatus badius* from Nyasoso and Mt. Cameroon. But according to the same author *Hybomys u. badius* and *H. u. univitattus* coexist in Mamfe region. Musser & Carleton (2005) mentioned taxonomic problems concerning the Central African *Hybomys* species, but confirmed three other forms in the Cameroon Highlands: *H. badius* on the Bakossi Highlands (Mt. Cameroon, Rumpi Hills), *H. eisentrauti* (described from Mt. Lefo, synonymized by Musser & Carleton with *H. badius*) on the Bamenda Highlands, and *H. basilii* on the Island of Bioko. Further revision and discoveries of new specimens from both lowland and highland forests of the CVL pending, we attribute the Mt. Kupe specimen from lowland forest provisionally to the *univitattus* complex.

Grammomys poensis (Eisentraut, 1965)

Three specimens were caught in lowland forest and cultivated areas at Nyasoso village (Table 2). One of the two males was sexually active and the female was pregnant, carrying two embryos and displaying 0+2 mammae. Specimens were identified based on their very long tail (Table 3), ending with a small tuft, and by typical skull characteristics, notably the globular aspect of the braincase, microdonty, as well as the existence of a stephanodont crest on the molar cusps and presence of a t7 on the upper M12 (see review in Petter & Tranier 1975). Comparison with *G. gazellae* (put in synonymy with *G. macmillani* by Musser & Carleton 2005) specimens from CAR and with *G. "rutilans"* (a synonym of *G. poensis*) from Gabon and with the holotype from Fernando Poo allows assignation of our new Kupe specimens to *G. poensis*. Yet, they are slightly smaller than the holotype which is a young adult. Two specimens were sequenced (cyt b) but a revision of the whole genus in West Africa is required before definite conclusions can be drawn. According to Eisentraut (1968) this species is absent from Mount Cameroon, but present in Mamfe (Sanderson 1940) and on Bioko Island (Eisentraut 1965).

Hylomyscus walterverheyeni Nicolas et al. 2008

Thirty-four specimens of this rodent were trapped on Mt. Kupe at different altitudes (Table 4). Among the 12 females we found two juveniles, the other being adult with

2+2 mammae. Three females were each carrying four to five embryos. Ten of the 20 males were sexually active. Our identifications were confirmed through molecular analyses (cyt b and 16S gene sequencing). According to our preliminary molecular analyses, specimens from Mt. Kupe are the sister clade of the newly described species *H. walterverheyeni* (Nicolas et al. 2008a, Missoup 2009). This species was described from the region between the Sanaga River and the Oubangui and Congo rivers in Cameroon, Gabon, Central African Republic and Republic of Congo. However, the authors stressed the importance of conducting additional sampling in Western Cameroon, Nigeria and the Dahomey Gap region in order to precisely define the western limit of its distributional range. Refined molecular analyses and multivariate morphometrical analysis of cranio-dental measurements are necessary to confirm whether the Kupe individuals represent a distinct montane forest clade.

Hylomyscus sp.

One adult female of *Hylomyscus* was captured in the zone under anthropogenic influence and was molecularly similar to four specimens called "*Hylomyscus* taxon 2" by Nicolas et al. (2006). These four specimens all came from the Korup National Park in western Cameroon. They undoubtedly belong to a new species. Waiting for a general revision of the genus and especially of the taxa found along the CVL, we provisionally call it "*Hylomyscus* sp." This female had a mammae formula of 2+2.

Mastomys natalensis (Smith, 1834)

One adult male specimen was trapped in Nyasoso village. An analysis of the cyt b gene confirmed its identification as *M. natalensis*. Because of the high morphological variability observed in this group and the low degree of specific distinctiveness (Denys et al. 2007), we did not compare this specimen with other specimens morphometrically. Previously only one specimen of this species was trapped (Eisentraut 1968), and therefore it does not seem to be common in the CVL while it is abundant in West Africa (Denys et al. 2005) and in Nigeria (Happold 1987).

Praomys Thomas, 1915

Based on molecular analyses and the identification key of Lecompte et al. (2001) the Mt. Kupe specimens belong to two different species. Eisentraut (1968) only recorded one *Praomys* species, *P. morio*, from Mt. Cameroon.

Praomys jacksoni (de Winton, 1897)

In our study this species is represented by one female, one male and one juvenile which were all trapped and brought to us by Nyasoso villagers (Table 4). The mammae formula was 1+2. This species is recognized by its well-developed supra-orbital crests and the presence of a clearly separated t3 on M1 (Lecompte et al. 2001). A comparison of our 16S and cyt b sequences with those published by Nicolas et al. (2005) and by Lecompte et al. (2002) confirmed our identification.

Praomys misonnei Van der Straeten & Dieterlen, 1987

Five females and eight males were trapped in the lowland forest (Table 2). Based on the absence of supra-orbital crests and their molar morphology they clearly belong to the so-called *tullbergi* complex. The females have a mammae formula of 1+2. A comparison of our 16S and cyt b sequences with those published by Nicolas et al. (2005) and Lecompte et al. (2002) confirmed our identification.

Subfamily Deomyinae Thomas, 1888

Deomys ferrugineus Thomas, 1888

Two specimens were captured at c. 1500 m asl on Mt. Kupe (Table 2). This is surprising since Eisentraut (1963) only obtained this species in the lowland forest, six specimens in Nyasoso and at "Lager V" (western part of Mt. Cameroon) at 600 m.

Lophuromys cf. ***sikapusi*** (Temminck, 1853)

We trapped only one male and one female; one badly damaged specimen (sex unknown) was brought to us by the villagers. All specimens were trapped in the village. They are characterized by a red belly and a short tail (Table 4). The female had 1+1 mammae. Recently, *Lophuromys* taxonomy and systematics in Central, West and East Africa has been under debate. According to Musser & Carleton (2005), the *Lophuromys sikapusi* complex may be represented in S Cameroon by different species, following Verheyen et al. (1997, 2000). Numerous sibling species are found within this complex. A molecular revision is necessary in order to precisely identify the specimens from Mt. Kupe.

Family Nesomyidae Major, 1897

Subfamily Dendromurinae G. M. Allen, 1939

Dendromus sp.

Only one adult male was captured in a crop field. According to Musser & Carleton (2005) and Eisentraut (1968, 1973), *D. messorius* in the Cameroon highlands is known from Manengouba and Nyasoso, and from the holotype from Efulen. The species is a typical inhabitant of tropical lowlands and lower mountain slopes. In the same region, Eisentraut found *Dendromus oreas* at higher altitudes (1850 m and 3000 m on Mt. Cameroon). MUSSER & CARLETON (2005) mentioned the high variability in *D. oreas* from West Central Africa. Our "new" specimen is smaller than *D. messorius* and *D. oreas* of the CVL. In size and skull morphology it is close to specimens in the Paris Museum from Belinga, Gabon, identified as *D. mystacalis*. The specimen from Mt. Kupe is also smaller than *D. messorius* from CAR. Pending further comprehensive revision of the genus in West-central Africa, we leave this specimen as unidentified.

Subfamily Cricetomyinae Roberts, 1951

Cricetomys cf. ***emini*** Wroughton, 1910

Four *Cricetomys* individuals (three males and one undetermined) were brought to us by hunters. They were obtained by traditional traps placed in Nyasoso village and in the forest near the top of the mountain, at approximately 1950 m asl. EISENTRAUT (1968) described 11 specimens from Buea, Nyasoso, Kumba and Mt. Cameroon as *C. gambianus poensis*. MUSSER & CARLETON (2005) put *poensis* in synonymy with *emini* and recognize *C. gambianus* only in the sub-Saharan savannah belt. Our specimens fit within the external measurements range of variability provided by EISENTRAUT (1968), except for the shorter tail length. According to OLAYEMI (2008) both *C. gambianus* and *C. emini* are present in South Nigeria. Further molecular work will help to refine the taxonomy within this genus.

Table 4. External measurements [mm] of Mt. Kupe *Crocidura*.

	HB	TL	HF	E	W
mean	94,2	53,4	14,6	8,6	16,7
range	82–105	48–62	10–17	7–11	13–19

Table 5. External measurements [mm] of Mt. Kupe Chiroptera.

Species	W	HB	TL	HF + claw	FA
Epomops 1	66	122	10	20 + 2	80
Epomops 2	50,5	113	16	20 + 2	77
Myonycteris	14	65		10 + 0,5	44

Order Soricomorpha Gregory, 1910

Family Soricidae G. Fischer, 1814

Crocidura cf. ***poensis*** (Fraser, 1862)

Five medium-sized shrews were captured in Sherman traps (Table 2). We recovered four males and one female with 0+2 mammae. At least eleven species of *Crocidura* are known from SW Cameroon (HUTTERER 2005). According to size and morphology our new specimens fit within the *C. poensis* complex (P. Barriere, pers. comm.).

It should be noted that EISENTRAUT (1973) recorded 5 species of shrews, *Sylvisorex megalura*, *Sylvisorex ollula*, *Crocidura nigeriae/poensis*, *C. attila*, and *C. hildegardeae* from Nyasoso at 850 m.

Order Chiroptera Blumenbach, 1779

We used mistnets to sample the bat population of a cave 950 m asl in the lowland forest of Mt. Kupe. Two fruit bat species were collected.

Family Pteropodidae Gray, 1821

Epomops franqueti (Tomes, 1860)

This species displays white basal ear tufts, and males also have white epaulets. We collected two adult females of this species (Table 5). This species was quite commonly trapped by EISENTRAUT (1968) on Mt. Cameroon and at Lake Barombi Mbo, and he attributed these specimens to the subspecies *franqueti*, mentioning the considerable variability of the species over all of West Africa. Our specimens from Nyasoso are much larger than the average for his specimens (FA=57,4, TL=12, HB=91, HF=15; EISENTRAUT 1968) but are smaller than Nigerian specimens (FA=82–91; HAPPOLD 1987).

Myonycteris torquata (Dobson, 1878)

One male of the little collared fruit bat was trapped. This species has also been sampled by EISENTRAUT (1968) at "Lager V" and "Lager VI" of Mt. Cameroon and was listed in an unpublished report by DOWSETT-LEMAIRE & DOWSETT (1998). Our specimen has a smaller forearm length (44 mm) than specimens from Mt. Cameroon (average 57,4 mm; EISENTRAUT 1968) and Nigeria (HAPPOLD 1987) (Table 5).

4. DISCUSSION

4.1. Rodent species diversity on Mt. Kupe compared to results of previous studies

Our study confirms the presence of *L.* cf. *sikapusi*, *L. striatus*, *M. setulosus*, *O. hypoxanthus*, *H.* cf. *univittatus* and *D. ferrugineus* on Mt. Kupe (Table 6). The differences between our species list and those of previous studies mainly concern genera for which the taxonomy is under revision: *Praomys*, *Hylomyscus*, *Mus*, *Nannomys* and *Cricetomys*. Concerning the genus *Praomys*, we could not confirm the presence of *P. morio* on Mt. Kupe, as suggested by EISENTRAUT (1968). This species was described from Mt. Cameroon where it ranges at altitudes up to 3000 m. The validity of *P. morio* was never assessed by molecular data. Our results show that the specimens from Mt. Kupe correspond to *P. misonnei*, not to *P. morio*. If future molecular studies confirm the validity of *P. morio* it should be restricted to the high altitudes of Mt. Cameroon. We also confirmed the presence of *P. jacksoni*, as mentioned by EISENTRAUT (1973) and DOWSETT-LEMAIRE & DOWSETT (1998). These authors also cited *Hylomyscus stella* from Mt. Kupe. However, NICOLAS et al. (2008b) showed that *H. stella* is restricted to East Africa, and that the specimens from West Central Africa (from the Sanaga River to the Oubangui-Congo River) represent a new species, *H. walterverheyeni*. Our results suggest that this species could also be present on Mt. Kupe. More detailed molecular and morphometrical analyses, though, are necessary to confirm this conclusion. EISENTRAUT (1968) attributed *Mus* specimens from Nyasoso to *M. setulosus*, which we confirm here on morphological and molecular grounds. Concerning *Cricetomys*, DOWSETT-LEMAIRE & DOWSETT (1978) mentioned the presence of *C. emini* at 1500 m. However, molecular analyses in progress seem to indicate quite a large genetic variability.

Our inventory adds three species to the fauna of the Mt. Kupe: *Grammomys poensis*, *Mastomys natalensis*, and *Hylomyscus walterverheyeni* (previously recorded under the name *H. stella*) (Table 6). Despite its presence on Mt. Cameroon, the genus *Mastomys* was not previously recorded on Mt. Kupe. Similarly, EISENTRAUT (1957, 1968) did not list *Grammomys poensis* but indicated that it was trapped by SANDERSON (1940) in the Mamfe region. We also confirm the presence of *Malacomys longipes*, *Oenomys hypoxanthus*, *Deomys ferrugineus,* and *Mus setulosus* in Nyasoso. We failed to collect *Stochomys longicaudatus* (4 specimens collected in Nyasoso by Eisentraut) and *Hylomyscus aeta,* both easily identifiable based on morphological characters. *Stochomys longicaudatus* is known to be present in fragmented populations throughout its distributional range, and may be locally abundant (KINGDON 1997). In the Kupe area this species may be rare or may even have disappeared since 1963.

Like DOWSETT-LEMAIRE & DOWSETT (1998), we found the bat species *Epomops franqueti* and *Myonycteris torquata* in a cave in the lowland forest of Mt. Kupe. EISENTRAUT (1973) and FEDDEN & MCLEOD (1986) collected both species at the same altitude. They seem to be quite common on Mt. Bakossi and Mt. Cameroon.

The yield of shrews was poor as compared to previous studies (EISENTRAUT 1973) and does not allow any conclusion.

Our study indicates that the rodent fauna on Mt. Kupe has not changed much since the pioneer study of EISENTRAUT (1957). This may be a sign of the quality of conservation of this forest. It has also shown that the rodent diversity is quite high in comparison with other mountains of the CVL (Mt. Bakossi, Mt. Manengouba, Mt. Lefo, Mt. Gotel, Mt. Cameroon – see MISSOUP et al. 2006). With 16 species, however, it is lower than on Mt. Oku (MISSOUP et al. 2006). This may be due to the fact that few inventories have been performed on these mountains. All mountains may harbour more species than are currently known. However, our results may also be biased by the common species because of the low number of individuals captured despite our trapping efforts. All the possible habitats of the lowland and montane forest were investigated but our trapping success remained very low in all lines and in all seasons (Table 2). Trapping success was lower than that obtained for Mount Elgon montane forest (7,7–10%) (KITYO & CLAUSNITZER 2001), Kilimandjaro (4,5–36 %) (MULUNGU et al. 2008) or montane forests of the Albertine Rift mountains, SW Uganda (3,41–11,4 %) (KASANGAKI et al. 2003). In all these studies, the highest trapping success was obtained in disturbed or degraded habitats.

4.2. Community analysis

It is generally assumed that the diversity of small mammals decreases with altitude, or at least changes with changes in vegetation type. Vegetation types may play a crucial role in structuring small mammal assemblages. In order to test if these hypotheses apply to Mt. Kupe we performed a correspondence analysis on presence-absence data for rodents and shrews as a function of altitudinal vegetation levels.

The graph of axis F1 x F2 of the correspondence analysis displays a quite good separation between all habitats (Fig. 1). It is clear that zones under direct human impact are well characterized by a cohort of commensals (like *Mastomys*, *Mus* and *Rattus*), but also species which are frequent in secondary forest and crops (e.g. *Lemniscomys*, *Lophuromys*, *Dendromus*, *P. jacksoni*). The true forest habitats display a different diversity with marked differ-

Table 6. Comparisons of the faunal lists for Mt. Kupe based on different studies (x= presence).

Species	**This study**	**Dowsett-Lemaire & Dowsett 1998**	**Eisentraut 1957**	**Eisentraut 1968, 1973**
Crocidura poensis	x	x	x	x
Crocidura attila		x	x	x
Crocidura sp.			x	
Cricetomys gambianus			x	x
C. emini	x	x		
Dendromus sp.	x			x
Grammomys poensis	x			
Lophuromys sikapusi	x	x	x	x
Deomys ferruguineus	x	x	x	x
Lemniscomys striatus	x	x	x	x
Mastomys natalensis	x			
Mus musculus	x			x
Mus setulosus	x	x		x
Mus musculoides		x	x	
Oenomys hypoxanthus	x	x	x	x
Praomys jacksoni	x	x		
Praomys morio			x	x
Praomys misonnei	x			
Hybomys cf. *univitattus*	x	x	x	x
Hylomyscus walterverheyeni	x	?		
Hylomyscus sp.	x			
Hylomyscus aeta			x	x
Hylomyscus stella?		x		
Malacomys longipes	x			
Stochomys longicaudatus			x	x
Rattus rattus			x	x
Micropterus pusillus			x	x
Epomops franqueti	x	x		
Myonycteris torquata	x	x		
Nannonycteris veldkampi?		x		
Lissonycteris angolensis		x		
Roussettus aegyptiacus		x		
Megaloglossus woermanni		x	x	x
Kerivoula smithii			x	x
Hipposideros caffer				x
Hipposideros ruber		x		
Hipposideros cyclops		x		
Rhinolophys alcyone		x		
Pipistrellus eisentrauti?		x		
Tadarida thersites?		x		

ences between the lowland forests on the one hand, and the sub-montane and montane forests (1500–2000 m) on the other along the F2 axis. *Hybomys*, *Hylomyscus* sp., *Malacomys*, and *P. misonnei* are characteristic of the lowland forest and are true forest taxa also found in the lowland forests of Gabon (Duplantier 1982; Nicolas & Colyn 2003). *H. walterverheyeni* and *Deomys ferrugineus* are the only species found at 1500 and 2000 m (upper sub-montane and montane forests) on Mt. Kupe. Eisentraut (1957) showed for Mt. Cameroon that *Malacomys* and *Deomys* are lowland forest taxa (< 900 m) and that only *Praomys morio* and *Hylomyscus aeta* reach the higher levels (up to 3100 m and 2000 m, respectively). Other species of *Hylomyscus* are commonly trapped at high altitudes in East Africa: On Mt. Elgon *H. denniae* is found in the forest and bamboo zones up to 2875 m and 3100 m (Kityo

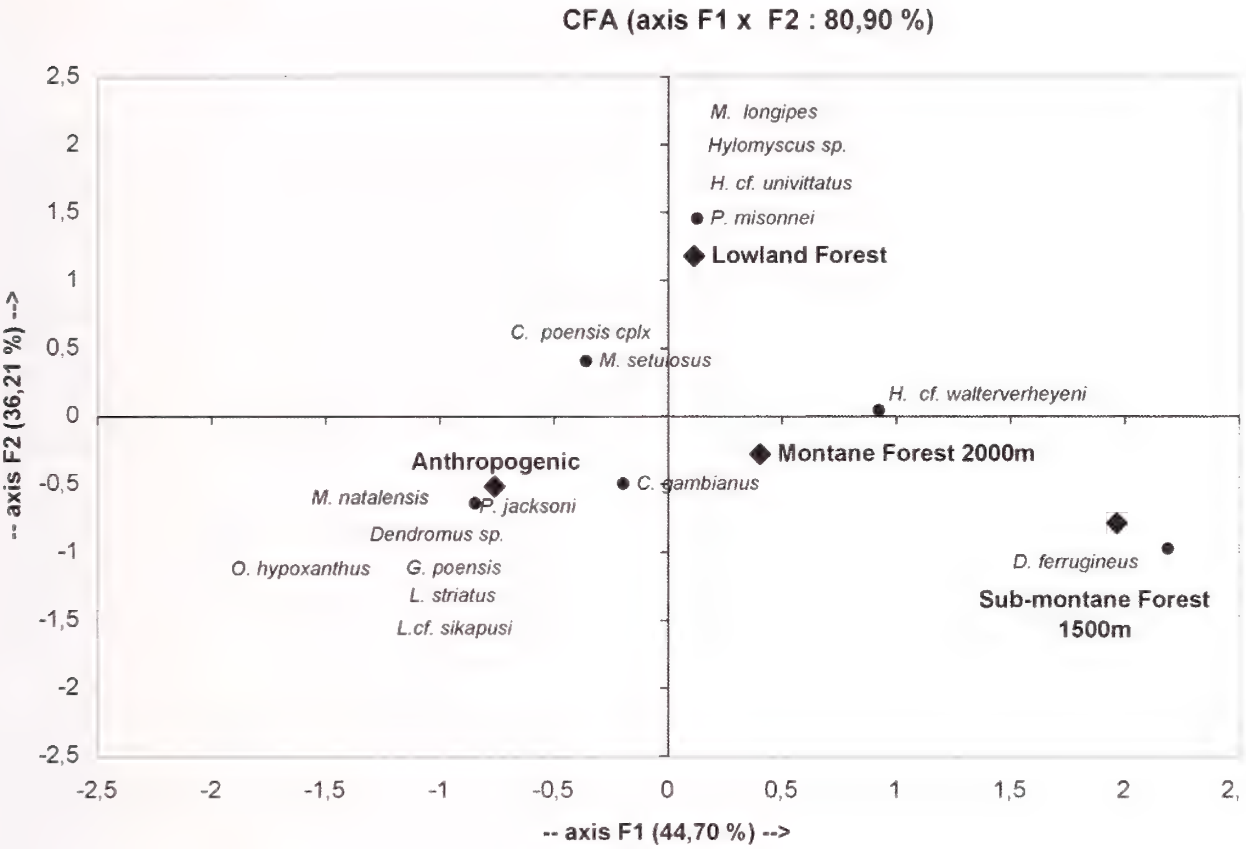

Fig. 1. Correspondence analysis scatter plot of axes 1 and 2 representing 80.9 % of the total variability based on presence-absence data for 16 species in the four general habitat types surveyed on Mt. Kupe.

& Clausnitzer 2001), while on Mount Rungwe *H. arcimontanus* is only found between 600 m and 2000 m (Carleton & Stanley 2005). In West and East Africa *Lophuromys roseveari*, *L. eisentrauti*, *L. flavopunctatus*, *Praomys jacksoni*, *P. morio*, *P. delectorum*, and *Colomys goslingi* are found above 2000 m (Dieterlen 1979; Verheyen et al. 1997; Kityo & Clausnitzer 2001; Mulungu et al. 2008).

In our study *Lophuromys* and *P. jacksoni* were only caught in zones under anthropogenic influence close to the village at around 800 m elevation. Eisentraut (1957) found *Stochomys*, *Cricetomys*, and *Dasymys* to be restricted to an altitude below 900 m, *Oenomys*, *Mus*, and *Lophuromys* reached 2100 m, and *Dendromus oreas* and *Otomys burtoni* were found above 2000 m. On Mt. Kupe we trapped *Deomys* at 1500 m, while *Cricetomys* is known from the summit (2000 m and above). On Mt. Elgon *Cricetomys* is also present at high altitude (3500 m) (Kityo & Clausnitzer 2001). In Bwindi, SW Uganda, species such as *Grammomys dryas*, *Hybomys* sp., *L. medicaudatus*, *rahmi*, *woosnami*, *H. aeta*, *denniae*, *vulcanorum*, *Mus bufo*, and *T. venustus* live in forests above 1800 m (Kasangaki et al. 2003). In lower elevation forests *H. stella*, *Praomys jacksoni*, *Praomys* sp., *S. longicaudatus*, and *T. kempi* occur. Other taxa like *Deomys*, *H. univittatus*, *O. hypoxanthus* found on Mt. Kupe, live in a wide range of habitats and may be found on the edge of forests.

Rodent species diversity in the area studied decreases drastically from lowland to sub-montane forest (Figure 1, Table 2) between 900 and 1500 m. This may correspond to the differences observed in vegetation composition. Both Letouzey (1985) and Tchiengue (2004) found floristic differences between the lowland forest and the montane forest, with some endemics occurring only above 1000m. Cheek et al. (2004) noted a floristic change from lowland to sub-montane forest on Mt. Kupe at 800 m. The very low diversity observed at 1500 m and 2000 m corresponds with the difference observed between a lower sub-montane forest (= very rich and diversified) and an upper sub-montane forest (= relatively poor) between 1400 m and 2000 m (Cheek et al. 2004). In comparing species turnover and elevation in small mammals for different tropical mountain regions MENA & VASQUEZ-DOMINGUEZ (2005) found the highest turnover at intermediate altitude between 1000 m and 2500 m, but they did not attempt to define causes of such changes in species diversity. EISENTRAUT (1957, 1968) also described a change in vertebrate community composition on Mt. Cameroon: for amphibians between 800 and 1000 m, for reptiles around 900 m, and for small mammals at 2100 m. Studies are on the way to verify the altitudinal effect hypothesis for the other mountains of the Bakossi and Bamenda Highlands of the CVL (MISSOUP et al., unpubl).

4.3. Conclusion

The results of our small mammal survey suggest an absence of rodent species endemic to the high altitude forest of Mt. Kupe. Because recent work has revealed an unsuspectedly high cryptic diversity, molecular analyses are now necessary to validate this hypothesis. Our study has updated the Mt. Kupe faunal list with the addition of four species not recorded in previous studies. The Mt. Kupe diversity is relatively high when compared to other Central African forest areas. We present first evidence that the recently described *H. walterverheyeni* occurs at 2000 m and is absent from habitats under impact by humans, and that *Deomys ferrugineus* can reach altitudes of 1500 m. On the other hand, *P. misonnei*, *Malacomys*, and *Hybomys* are restricted to lowland forest below 900 m. We recovered almost all the true forest species previously collected from Mt. Kupe, suggesting a good preservation of the lowland forest. This is of importance for drill conservation because these primates have been encountered on Mt. Kupe from 700 m up to 2000m and they use all types of habitats on Mt. Kupe. Of the species previously mentioned for this area by Eisentraut we could not collect *Stochomys longicaudatus* and *Hylomyscus aeta* during this study. These two genera are inhabitants of the lowland forests of Central Africa. Little is known about their habitats and demography; their conservation status is 'Lower Concern' (BOITANI 2007; SCHLITTER & VAN DER STRAETEN 2007). The absence of *S. longicaudatus* and *H. aeta* may suggest a low population size. Moreover, the low trapping success we obtained during various seasons may indicate a general decrease of rodent abundance. This ought to be checked in the future because it may indicate an over-exploitation of forest rodents for bushmeat.

We observed a change in the small mammal community composition between lowland and sub-montane forest, suggesting a turnover occurring between 1000 m and 1500 m. We also observed a change in the community structure between areas under human impact and lowland forests, with different genera or species present and a rather good diversity in the undisturbed lowland forest. This stresses the importance of regular small mammal biodiversity surveys in close relationship with local vegetation associations on Mt. Kupe and more generally in hotspot zones to follow the forest condition.

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Zusammenfassung. Mehr als 50 Jahre nach M. Eisentrauts erster Bestandsaufnahme der Kleinsäuger-Fauna des Mount Kupe, SW Kamerun, unternahmen wir die zweite. Dabei konnten wir 19 Arten nachweisen: 16 Nager, zwei Fledermäuse, eine Spitzmaus. Für jede Art werden Daten zur Biologie, Verbreitung und Taxonomie zusammengefasst. Zwischen der Nager-Artengemeinschaft des Tieflandes (< 1000 m) (inkl. *Praomys misonnei*) und der der höher gelegenen Wälder (1500–2000 m) (inkl. *Hylomyscus* cf. *walterverheyeni* als Erst-Nachweis für das Kameruner Bergland) bestehen Unterschiede, die wahrscheinlich mit den bekannten Veränderungen der Vegetation zwischen 1000 und 1500 m Meereshöhe zusammenhängen. In bewohnten und landwirtschaftlich genutzten Gebieten am Fuße des Mount Kupe konnten wir acht weitverbreitete Nager-Arten nachweisen. Bei einigen Arten der montanen Waldgebiete bestehen weiterhin taxonomische Probleme.

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A new species of *Surdisorex* Thomas, 1906 (Mammalia, Soricidae) from western Kenya

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Abstract. The genus *Surdisorex* represents Kenya's only endemic genus of mammal. It has heretofore included two species from the highlands of central Kenya. Here we add a third species, also from Kenya, based on a specimen from the ericaceous zone of the eastern slopes of Mt. Elgon. Although this species further aligns Mt. Elgon with the Kenya Highlands, the mammal fauna of Mt. Elgon illustrates a mixture of faunal origins and associations.

Keywords. *Surdisorex*, mole shrews, endemism, fossorial mammals, Mt. Elgon.

1. INTRODUCTION

In 1906, Thomas erected the genus *Surdisorex* for a highly specialized burrowing shrew, without external pinnae, from the Aberdare Mountains of central Kenya. Ten years later, a second species of the genus was named by HOLLISTER (1916) from nearby Mt. Kenya. For over 100 years, the genus *Surdisorex* has been Kenya's only endemic genus of mammal. Even with the acquisition of large series of each taxon, the two species remain readily diagnosable despite their geographic proximity. HOLLISTER (1918) stated that both species were confined to high altitudes (above 9,000'). Their occurrence on mountain tops appears to account for their isolation and distinction, despite a geographic disjunction of less than 50 miles.

In 1984, a specimen of the genus *Surdisorex* was picked up on a footpath in the ericaceous zone of the Kenyan slope of Mt. Elgon. We describe it as a third member of the genus *Surdisorex*. It is surprising that this distinctive animal had gone uncollected from this often-studied mountain until now.

2. MATERIALS AND METHODS

The sole representative of the new species was found dead on the footpath by Dr. Henning Grossman at 3,150 m in the ericaceous zone of Mt. Elgon in December, 1984 and donated to Professor Kim M. Howell, Department of Zoology, University of Dar es Salaam who assigned it the field number KMH 3213. Professor Howell donated the specimen to the Field Museum of Natural History in 2005. The specimen was partially eviscerated with the loss of internal viscera and external reproductive organs, but we do not know how or when this occurred. It was kept in the Tanzanian collection, and stored in ethanol for some 20 years under the name '*Myosorex* sp.' Exposure to light may have discolored the pelage.

We compared the specimen with specimens in the American Museum of Natural History (AMNH), The Natural History Museum, London (BMNH), Field Museum of Natural History, Chicago (FMNH), the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK). The following external measurements were recorded for each specimen: total length (TOL; tip of nose to end of caudal vertebrae), head and body length (HB; tip of nose to base of tail), tail length (TL; from base of tail to end of caudal vertebrae), hind foot length (HF; from heel to tip of claw), ear height (E; the longest dimension of the opening of the auditory meatus) and weight (WT). All measurements are in mm except weight (grams), and generally follow DEBLASE & MARTIN (1974). The cranial and dental variables measured are condylo-incisive length (CI), post-palatal length (PPL), length of entire upper toothrow (UTR), length of complex teeth in upper toothrow, i.e. the distance from the anterior edge of the fourth upper premolar to the posterior edge of the third upper molar (P^4-M^3), distance from anterior edge of first upper incisor to posterior edge of upper canine (UNICUSP), width of third upper incisor (I^3W), width of canine (CW), length of third upper molar (M^3L), width of third upper molar (M^3W), least interorbital width (IO), bimaxillary width (MX), greatest width of the braincase (GB), post-glenoid width (PGL), height of the cranial capsule (HCC), length of mandible including the incisor (md), height of coronoid process on dentary (cor), and length of lower toothrow (ltr). These variables are a subset of those utilized by Hutterer & Kock (2002), Dippenaar (1977), and Carraway (1990) and are figured in Stanley et al. (2005). The infraorbital bridge was measured at its narrowest point; the structure was figured by Meester (1963). Digital callipers were used to measure skulls to the nearest 0.01 mm.

Standard descriptive statistics (mean, range, and standard deviation) were calculated for each species. One-way analysis of variance (ANOVA) was used to determine whether there were significant differences in cranial characters between sexes in each species. Principal components were extracted from a variance-covariance matrix using the cranial variables converted to natural logarithms. All univariate and multivariate statistical analyses were conducted using Systat (version 11.00, 2004).

3. RESULTS

External measurements indicate that *S. polulus* has a shorter head and body, but longer tail and hindfoot than *S. norae* (Table 1). Unfortunately, no external measurements were recorded from the specimen found on Mt. Elgon at the time of collection. The tail and hindfoot measurements taken from the preserved specimen indicate this specimen had a longer tail than either of the other two species, but the hindfoot length was intermediate between *S. norae* and *S. polulus*.

In general, the specimen from Mt. Elgon falls between the means of *S. norae* and *S. polulus* in various length measurements of the skull (Table 2). One-way Analysis of Variance indicated there was no sexual dimorphism in cranial characters between sexes in either *S. norae* or *S. polulus*. The one exception was in *S. norae*, where the males had a longer toothrow on the dentary than females ($F = 5.14$; $P \leq 0.05$). Based on the fact that this was the only character exhibiting significant differences between sexes, and that this difference was found in only one species, the sexes were combined in all other analyses.

Table 1. External measurements (in mm) for samples of *Surdisorex*, given as mean, standard deviation, range and sample size. Measurements of *S. norae* and *S. polulus* taken from specimens upon capture, and those of *S. schlitteri* from the preserved specimen.

External measurement	Head & body	Tail length	Hindfoot
Surdisorex norae	102.2 ± 4.1 95–110 n = 19	28.2 ± 3.5 21–33 n = 19	15.6 ± 1.2 14–17.5 n = 19
Surdisorex polulus	94.8 ± 3.1 89–100 n = 11	28.5 ± 2.3 24–31 n = 11	16.5 ± 0.5 16–17 n = 11
Surdisorex schlitteri	–	28.6	16.1

Principal components analysis resulted in skull length measurements generally having positive and moderately high loadings with the first component. For example, the variable with the highest loading on PC 1 was the condylo-incisive length (CI). PC 2 was most heavily influenced by the length of the row of upper unicuspids (length from first upper incisor to the canine), which had positive loadings. Equally influential on the second component (but with negative loadings), was the width of the third upper incisor (I^3W). The third component was most influenced by the width of the third upper molar, (M^3W) which exhibited negative values. The first three components explained 40.1, 22.3 and 16.1% of the variation, respectively. A plot of the specimen scores on the first two components extracted is shown in Fig. 1.

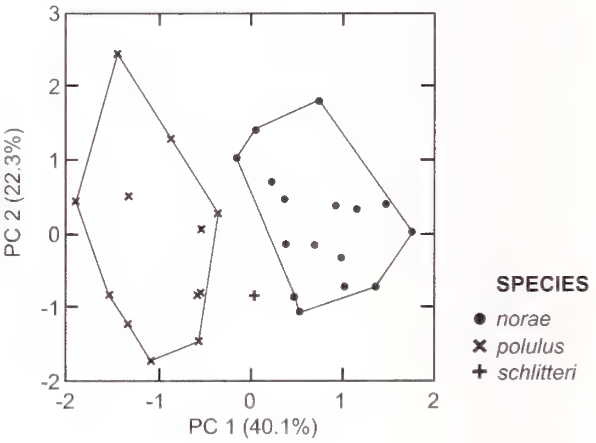

Fig. 1. Plot of the specimen scores on the first two principal components, based on cranial measurements.

Table 2. Comparison of selected cranial measurements (mm) for 3 species of *Surdisorex*, given as mean, ± standard deviation, sample size and range.

Character	*S. schlitteri* (n = 1)	*S. norae*	*S. polulus*
Condylo-incisive length (CI)	25.15	25.79 ± 0.37 (n = 13) 25.24–26.75	24.68 ± 0.30 (n = 8) 24.35–25.06
Post-palatal length (PPL)	11.28	11.38 ± 0.24 (n = 10) 11.05–11.86	10.99 ± 0.21 (n = 7) 10.59–11.25
Upper toothrow length (UTR)	10.55	11.03 ± 0.22 (n = 21) 10.55–11.48	10.43 ± 0.20 (n = 18) 10.01–10.75
Length of P^4-M^3 (P^4-M^3)	6.10	6.28 ± 0.15 (n = 17) 6.02–6.59	6.02 ± 0.14 (n = 15) 5.81–6.29
Length of upper unicuspids (UNICUSP)	4.45	4.75 ± 0.13 (n = 17) 4.53–5.02	4.40 ± 0.14 (n = 15) 4.13–4.61
Greatest width of upper I^3 (I^3W)	0.72	0.71 ± 0.05 (n = 17) 0.62–0.76	0.70 ± 0.05 (n = 15) 0.61–0.79
Greatest width of upper canine (CW)	0.77	0.82 ± 0.04 (n = 17) 0.72–0.87	0.78 ± 0.03 (n = 15) 0.72–0.84
Greatest length of upper M^3 (M^3L)	1.62	1.58 ± 0.07 (n = 17) 1.42–1.68	1.49 ± 0.08 (n = 14) 1.40–1.68
Greatest width of upper M^3 (M^3W)	0.87	0.87 ± 0.05 (n = 17) 0.80–0.97	0.84 ± 0.05 (n = 15) 0.76–0.94
Interorbital width (IO)	5.43	5.30 ± 0.14 (n = 16) 5.08–5.50	5.22 ± 0.19 (n = 13) 4.82–5.54
Maxillary breadth (MX)	7.00	7.26 ± 0.18 (n = 20) 6.93–7.56	6.84 ± 0.16 (n = 18) 6.53–7.12
Greatest breadth of cranium (GB)	12.90	13.17 ± 0.29 (n = 13) 12.50–13.72	12.50 ± 0.20 (n = 9) 12.04–12.68
Post-glenoid width (PGL)	8.10	8.29 ± 0.25 (n = 17) 7.86–8.76	7.98 ± 0.18 (n = 11) 7.59–8.18
Height of cranial capsule (HCC)	6.23	6.62 ± 0.18 (n = 16) 6.36–7.03	6.38 ± 0.19 (n = 8) 6.03–6.60
Length of mandible (md)	16.41	16.58 ± 0.36 (n = 20) 15.83–17.34	15.81 ± 0.17 (n = 17) 15.58–16.28
Coronoid height (cor)	6.70	6.64 ± 0.22 (n = 21) 6.36–7.13	6.41 ± 0.17 (n = 18) 6.17–6.73
Lower toothrow length (ltr)	9.70	9.99 ± 0.19 (n = 21) 9.65–10.42	9.46 ± 0.19 (n = 18) 9.13–9.71

3.1. The Mt. Elgon Mole Shrew

Surdisorex schlitteri n. sp.

Holotype. FMNH 195069 (KMH 3213). Old adult, teeth heavily worn, sex indeterminate although suspected to be male since no teats are visible. Secondary number KMH 3213. Collected by H. Grossman in December 1985. Specimen prepared as fluid-preserved body with skull removed.

Type locality. Kenya, eastern flank of Mt. Elgon, ericaceous zone at 3,150 m.

Etymology. The specific epithet honors Dr. Duane Schlitter, recognizing his important contributions to the knowledge of African small mammals and his personal and scientific engagement in Kenya.

Diagnosis. Intermediate in cranio-dental dimensions compared with the other two species in the genus, *S. polulus* and *S. norae*. Braincase smaller and absolutely shorter. The more anterior position of the pair of anterior palatal foramina is unique within the genus, as is the position of the last palatal foramen, situated between the second pair of unicuspids. Infraorbital bridge narrow. The lingual extension of the upper P^4 is longer than in the other

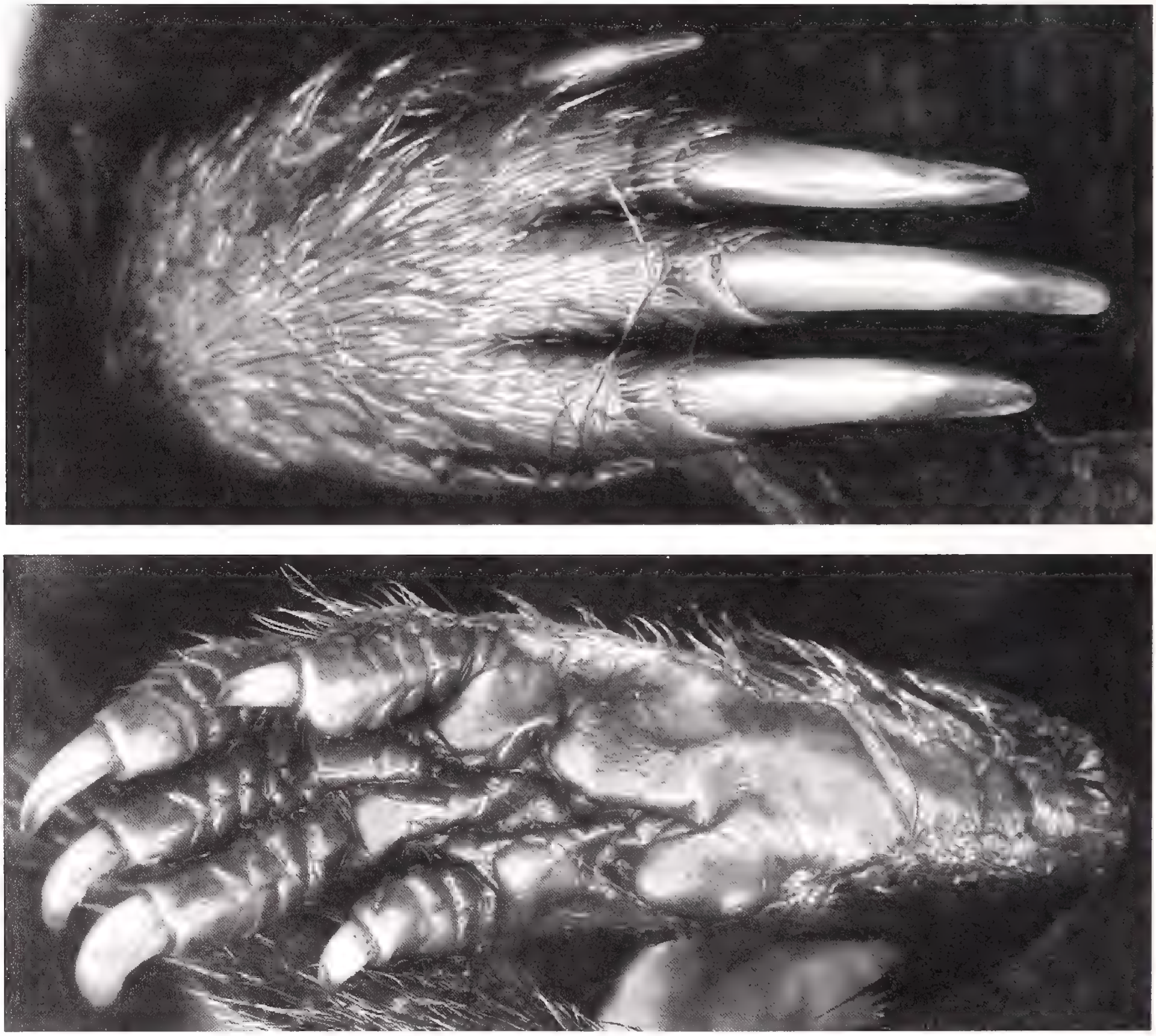

Fig. 2. Fore- and hindfoot of the holotype specimen of *Surdisorex schlitteri* n. sp. (FMNH 195069); length of hindfoot (including claws) is 16.1 mm.

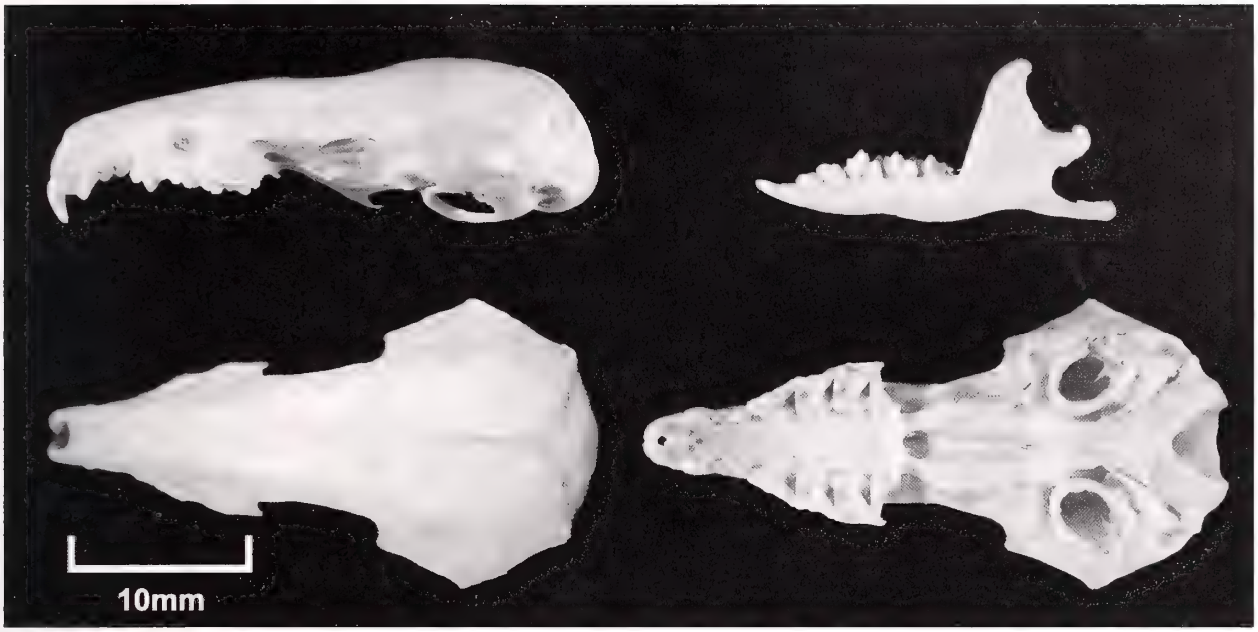

Fig. 3. Skull of *Surdisorex schlitteri* n. sp. (FMNH 195069, holotype); cranium in lateral, dorsal and ventral view, mandible in lateral view.

members of the genus, and almost in contact with the anterior edge of M^1. Lower P_4 narrow. Mandibular condyle heavy and straight-sided, forming a near-triangle without sinuosity.

Description. The new species exhibits characters typical for the genus. The tail is short (28.6/84=34% of Head and Body). Fur is thick and woolly, length of single hairs on dorsum 9 mm. Color faded, presumably because of long-term preservation in alcohol, base of hairs dark brown, terminal 2 mm lighter. The foreclaws greatly enlarged, hindclaws moderately so (Fig. 2). Ear conch absent. Eyes reduced and covered in membrane. Skull hexagonal, typical of burrowing Soricidae (e.g. *Myosorex*, *Anourosorex*, *Blarina*) with particularly well-defined anterior facets of the braincase (Fig. 3). Interorbital region elongate (between posterior processes of maxilla and anterior aspect of the braincase). Bridge across infraorbital foramen narrow (1.87 mm). Nuchal crests well-developed, sagittal crest slight. Braincase small and short, as reflected in the measurement from the anteromost corner of the braincase to the corresponding occipital condyle and in the distance of the antero-lateral component of the hexagon-shaped braincase. Foramen magnum oval-shaped. Paired frontal foramina within interorbital basin. This basin provides a sinuous curve to the lateral profile of the skull.

Three upper and two lower unicuspids, both unicuspid rows void of the vestigial unicuspids typical of *Myosorex*. Unicuspids broad, each with a medial accessory cusplet. Protocone of P^4 very prominent, forming a prominent shelf with parastyle. Upper M^1 and M^2 without metaloph. Lower incisor denticulate, with chisel-like tip. Mental foramen beneath second cusp of lower P_3. Lower P_4 fairly narrow, exhibiting the inverted v-shape pattern typical of the Myosoricinae (HUTTERER et al. 2002). Lower M_3 with well-developed and deep entoconid basin (MEESTER 1963).

MEESTER (1958) found that palatal foramina are useful in distinguishing closely related species of primitive African Soricidae (i.e. *Myosorex*). For the new taxon, the three principle anterior incisive foramina are tightly clustered in a triangle. The anterior pair is positioned slightly anterior to the medially positioned third member of this triad, this pair being located in a plane even with the anteromost portion of the first unicuspid (Fig. 3). The third foramen of this triad is positioned just below the anterior pair and is still situated within the anterior half of the first unicuspid. These foramina are followed by two reduced foramina, located approximately midway down the first unicuspid. A final foramen, the sixth, is located midway down from the second unicuspid.

4. COMPARISONS

In most cranio-dental measurements, *Surdisorex schlitteri* is intermediate in size between *S. norae*, the largest member of the genus and *S. polulus*, the smallest (Table 2). This

Table 3. Comparison of selected cranial measurements (mm) for 3 species of *Surdisorex*, given as mean, ± standard deviation, range and sample size.

Character	*S. norae*	*S. polulus*	*S. schlitteri*
Condylo-incisive length	25.8 ± 0.3 25.2–26.7 (n = 21)	24.6 ± 0.3 23.8–25.1 (n = 15)	25.1
Post-palatal length	11.4 ± 0.2 11.0–11.9 (n = 18)	10.9 ± 0.3 10.5–11.2 (n = 13)	11.3
Upper toothrow length	11.0 ± 0.2 10.6–11.5 (n = 21)	10.4 ± 0.2 10.0–10.7 (n = 15)	10.5
Length of P^4-M^3	6.3 ± 0.2 6.0–6.6 (n = 18)	6.0 ± 0.1 5.8–6.3 (n = 14)	6.1
Length of upper unicuspid teeth	4.9 ± 0.2 4.6–5.5 (n = 18)	4.6 ± 0.4 4.2–5.4 (n = 14)	4.4
Greatest width of upper I^3	0.7 ± 0.0 0.6–0.8 (n = 18)	0.7 ± 0.1 0.6–0.8 (n = 14)	0.7
Greatest width of upper canine	0.8 ± 0.0 0.7–0.9 (n = 18)	0.8 ± 0.0 0.7–0.8 (n = 14)	0.8
Greatest length of upper M^3	1.6 ± 0.1 1.4–1.7 (n = 18)	1.5 ± 0.1 1.4–1.7 (n = 14)	1.6
Greatest width of upper M^3	0.9 ± 0.1 0.8–1.0 (n = 18)	0.8 ± 0.0 0.8–0.9 (n = 14)	0.9
Interorbital width	5.3 ± 0.2 5.1–5.6 (n = 21)	5.3 ± 0.2 5.0–5.6 (n = 15)	5.4
Maxillary width	7.3 ± 0.2 7.0–7.6 (n = 21)	6.9 ± 0.2 6.5–7.2 (n = 15)	7.0
Greatest width of cranium	13.2 ± 0.3 12.5–13.7 (n = 18)	12.6 ± 0.3 12.0–13.2 (n = 15)	12.9
Post-glenoid width	8.3 ± 0.2 7.9–8.9 (n = 21)	8.0 ± 0.2 7.6–8.5 (n = 15)	8.1
Height of cranial capsule	6.7 ± 0.2 6.4–7.0 (n = 21)	6.4 ± 0.2 6.0–6.7 (n = 14)	6.2
Length of mandible	16.6 ± 0.3 16.1–17.3 (n = 21)	15.8 ± 0.1 15.5–16.0 (n = 15)	16.4
Coronoid height	6.6 ± 0.2 6.3–7.0 (n = 21)	6.4 ± 0.2 6.0–6.8 (n = 15)	6.7
Lower toothrow length	10.0 ± 0.2 9.6–10.4 (n = 21)	9.4 ± 0.2 9.1–9.7 (n = 15)	9.7

intermediate position is reflected in its position between the other two species along the primary axis of the first Principle Component (Fig. 1), an axis that illustrates size differences. Its infraorbital bridge is narrower (1.87) than either *norae* (1.97 and 2.26) or *polulus* (2.13 and 2.16). Its mandibular condyle is heavy and straight-sided and more or less triangular, without the sinuosity seen in the other two species.

The new species can be distinguished from *S. polulus* by its generally larger size in most cranial and dental dimensions (CI, MX, GB, md, ltr: Table 2). In the new species, the central foramen of the anterior triad is located posterior to the triad pair whereas in *S. polulus*, it is situated slightly ahead, between the incisor and the first unicuspid. The second pair of palatal foramina is in a comparable position between these species, but in the new species, the sixth and postero-most palatal foramen is located between the second unicuspids instead of between the first and second unicuspids, as in *S. polulus*.

From *Surdisorex norae*, the new species can be distinguished by its generally smaller size in most dimensions: (CI, MX, GB, I1-P3 length, ltr; Table 2). In the new form, the antero-lateral dimension of the hexagonal edge of the braincase is 4.63, compared with 4.79 and 5.15 in *S. norae*. The distance from the antero-lateral corner of the braincase to the corresponding occipital condyle is 10.11 vs. 10.18 and 10.93 in *S. norae*. The lower P_4 is narrower than in *S. norae*.

The shorter length of the upper unicuspids in the new species gives them a relatively broader apppearance than those of *S. norae*. This is especially clear in the first and third unicuspids. The angle in the posterior fovea of the upper P^4 is about 90° in the new form vs. 120° in *Surdisorex norae*; therefore there is no medial gap between the P^4 and M^1 in the new form compared with *norae*.

The anterior pair of palatal foramina in *Surdisorex norae* is positioned more posteriorly than in the new species, such that they form a straight line across the anterior half of the first unicuspid. The next pair is positioned comparable to the condition seen in the new species, whereas the final foramen is located midway down the third unicuspid.

A distinct sinus canal foramen (MEESTER 1963) is visible on the left side of the pterygoid region of the new species. It is less well-developed but evident on the right side. In other members of the genus, a canal replaces the foramen. A larger series is necessary to determine the significance of this feature.

There is no east to west size cline among the species of *Surdisorex*, further demonstrating their mutual distinction. The largest species is *Surdisorex norae* from the Aberdare Mountains, which is located between the populations of *S. schlitteri* and *S. polulus*.

Ecology of *Surdisorex* spp. The ecology of *Surdisorex* spp. is poorly known; to date there has only been a single published paper on the subject (DUNCAN & WRANGHAM 1971). We have little data to report for *S. schlitteri*. Represented by a single specimen, *S. schlitteri* is only known from the ericaceous zone of Mt. Elgon. The Kenyan slope of Mt. Elgon was specifically surveyed for subterranean insectivores by DUNCAN & WRANGHAM (1971) without finding this species. However, these authors note that on Mt. Elgon, burrows of the golden mole (*Chrysochloris stuhlmanni fosteri*; species rank suggested by THORN & KERBIS PETERHANS 2009) are 'common in fairly open ground in the ericaceous zone up to 10,000 feet <3048m>'. The golden mole is known from the ericaceous zone of Mt. Elgon and the nearby Cherangani Hills. The study of DUNCAN & WRANGHAM (1971) showed that *Chrysochloris fosteri* feeds mainly on earthworms, supplemented by smaller oligochaetes. Earthworms were predominant in the diet of *S. norae* (Aberdares range) and *S. polulus* (Mt. Kenya). They concluded that *Surdisorex* and *Chrysochloris* share an earthworm diet and mole-like habits. In turn, this may have contributed to ecological displacement, mutually excluding these vermivores from overlapping ranges during times of climatic amelioration. Though this is a reasonable conclusion, the new record of *S. schlitteri* contradicts this view. The occurrence of *S. schlitteri* on Mt. Elgon also calls into question the recognition of *Chrysochloris* vs. *Surdisorex* burrows by visual recognition alone.

Reporting on the Oxford University Expedition of 1969, DUNCAN & WRANGHAM (1971) documented *S. norae* and *S. polulus* in bamboo, mixed *Podocarpus*/bamboo and swamp. In the Aberdares, *S. norae* was collected at Kiandongoro Gate (specimens in BMNH) along a swamp in moorland at 9,400' (=2,865 m). Our 2006 efforts (JCK, TCD, BA) documented a single *S. norae* on the Aberdares at 2,700 m (=8860') in secondary forest, the lowest vouchered record for the genus, but none at 2,200 m (=7220'). During our surveys, *S. norae* was extremely common at 3,300 m (10,830') in *Hagenia* forest, *Carex* tussock grass and alpine shrubs and meadows. Heller collected *S. norae* on the summit of the Aberdares at 11,000' (specimens at USNM; Appendix). Our collated data (Appendix) indicates that *S. norae* ranges between 2,700 m and 3,350 m.

With a single exception, all records of *S. polulus* originate from the west slope of Mt. Kenya. This may be an artefact of site access and collecting bias. The lowest record from Mt. Kenya (AMNH 82479) is at 9,000' (2,743 m) and the highest records are from 12,100' (= 3,690 m, USNM records). Records of *S. polulus* from Mt. Kenya in the BMNH collected by the Oxford Expedition of 1969 originate near the Naro Moru Track at 10,500' (= 3,200 m). They derive from a range of bamboo associated habitats including mixed bamboo, bamboo/*Podocarpus* forest, bamboo mixed with 6" grass and swamp near bamboo (Oxford Expedition of 1969, specimens in BMNH). LORING (1910) describes them as common in grassy openings within bamboo thickets at 10,000'. At other elevations (10,700' and 12,100') they frequented *Otomys* sp. runs in tall marsh grass.

5. DISCUSSION

This remarkable discovery suggests a relictual biotic association between Mt. Elgon and the nearby Kenyan Highlands to the east (The Aberdares and Mt. Kenya). The three known species of *Surdisorex* ssp. are confined to upper montane forest (uncommon), bamboo, and ericaceous and alpine zones above 2,700 m. The three taxa are mutually isolated due to their confinement to high montane habitats.

Mt. Elgon has been well surveyed over the past 100 years. For the Ugandan slope, this includes: LOVERIDGE in 1933–1934 (ALLEN & LAWRENCE 1936), DAVENPORT et al. (1996); CLAUSNITZER & KITYO (2001); CLAUSNITZER (2003); CLAUSNITZER et al. (2003). In addition to the report of DUNCAN & WRANGHAM (1971), historical expeditions to the Kenyan slope of Mt. Elgon to collect small mammals include those of KEMP in 1909 (reviewed in LOVERIDGE 1937), BAYER in 1914 (LONNBERG 1918), the Swedish Expedition of 1920 (GRANVIK 1924), and LOVERIDGE in 1934 (ALLEN & LAWRENCE 1936). The absence of *Surdisorex* in prior reports is surprising. The genus is extremely common in bamboo/alpine zones of the Aberdares and Mt. Kenya. Perhaps its co-occurrence with *Chrysochloris fosteri* on Mt. Elgon limits its abundance.

Mt. Elgon lies at the confluence of three major faunistic regions: the Albertine Rift and Congo basin to the west, the Kenya Highlands to the east, and the northern highlands of Tanzania to the south. It houses representatives of two or three of these systems (summarized in CARLETON et al. 2006): *Sylvisorex granti* group, *Colomys goslingi* (Ruwenzoris, Albertine Rift); *Crocidura elgonius, Crocidura fumosa, Surdisorex* sp., *Rhabdomys dilectus*, and possibly *Cricetomys ansorgei* (Kenya Highlands); and perhaps from the third as well (northern highlands of Tanzania): *Lophuromys aquilus* (MUSSER & CARLETON 2005), *Hylomyscus anselli* (BISHOP 1979). Mt. Elgon also houses a few strict endemics of its own (*Otomys barbouri, Otomys jacksoni*). Although our knowledge of the alpha taxonomy of the small mammals in the region is incomplete, the central position of this extinct volcano reflects influences from multiple montane biotic systems.

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Zusammenfassung. *Surdisorex* ist die einzige endemische Säugetiergattung Kenias. Bisher enthielt die Gattung zwei Arten, die in den zentralen Hochländern Kenias beheimatet sind. Hier fügen wir eine dritte Art hinzu, ebenfalls aus Kenia, basierend auf einem Exemplar von der Ericaceen-Zone der Ostflanke des Mount Elgon. Diese neue Art, *Surdisorex schlitteri* n. sp., verbindet Mount Elgon zoogeografisch mit den Hochländern Kenias, doch weist die Säugetierfauna des Mount Elgon auch eine spezielle Mischung faunistischer Einflüsse auf.

APPENDIX

Specimens examined. *Surdisorex norae* (THOMAS, 1906): all records from Aberdare Mountain NP, Kenya. AMNH 187262, 8 mi W of Bellevue (female); BMNH 6.7.8.1 (type), east side, near Nyeri, 9500', old female; BMNH 10.5.3.1, 11,000' (female); BMNH 1974.653-74.657, Kiandongoro Gate, 9,400' (3 females, 2 males); FMNH 190257-190266, FMNH 190623-190626, 28.5 km W & 4.9 km N of Nyeri, 3,100 m (6 males, 8 females), FMNH 190622, 3.8 km W & 2.5 km S of Gatarakwa, 2,700 m (male); USNM 165513-166515, (1 female, 2 males), 182581-182586, summit, 11,000' (2 females, 4 males), USNM 589811-589813, USNM 589815-589818, Fishing Lodge, 9,000'–9,500' (1 female, 6 males).

Surdisorex polulus (Hollister, 1916): all but AMNH record, from W slope, Mt Kenya, Kenya. AMNH 82479, E slope, 9,000' (female); BMNH 1974.646-1974.652, Naro Moru Track, 10,500' (3 females, 2 males, 2 ?); FMNH 43845=USNM 163980, 12100' (female), FMNH 43846=USNM 163983, 12100' (male); USNM 163975-163979 (4 males, 1 female), USNM 163981-163982 (2 females), USNM 163984 (male), USNM 163986-163991 (3 males, 3 females), USNM 163993-163994 (male, female), USNM 163997-163998 (male, female), USNM 164000 (female), USNM 164003-164004 (2 females), USNM 165509 (male), USNM 165511 (female), 9000'-12100', USNM 589820, Naro Moru Gate, 10000' (male); ZFMK 2003.702 (female), Mt Kenya N.P., 2950 m, Chagoria trail.

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Climbing mice of the genus *Dendromus* (Nesomyidae, Dendromurinae) in Sudan and Ethiopia, with the description of a new species

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Abstract. The species of *Dendromus* occurring in Sudan and Ethiopia are revised. The forms of climbing mice referred to *Dendromus mystacalis* (Heuglin, 1863) from Sudan and other parts of Africa are compared with the typical population from Ethiopia. Ethiopian *D. mystacalis* differ from the other African populations in morphology and habitat. On the other hand, all populations from outside Ethiopia correspond in size and appearance and live in similar habitats. It is suggested that the lowland populations represent a different species. A new species, *Dendromus ruppi*, is described from the Imatong Mts., Sudan. It is a relatively large montane form, which was isolated during climatic changes in a Pleistocene postpluvial phase, and is probably endemic to these mountains.

Keywords. Sudan, Ethiopia, rodents, *Dendromus*, morphology, ecology, altitudinal distribution, habitat, new species.

1. INTRODUCTION

The genus *Dendromus* (African Climbing Mice) contains at least 12 species distributed throughout sub-Saharan Africa. Most species occur in S, C and E Africa (Musser & Carleton 2005). Typical habitats are long grassland, bracken, dense scrub, grassy wetland, and subalpine or alpine vegetation.

Species are characterised by small size, soft brown or reddish-brown pelage and a long thin tail (100–160% of head and body length, depending on the species) and feet specialised for climbing. Several species have a black mid-dorsal stripe, and one has three black stripes. In some species the stripe is barely visible or even absent.

Most species of *Dendromus* climb with the aid of the long digits of the forefeet and hind feet. The opposable digit 5 of the hindfoot which can be opposed to contact digit 1 and the prehensile tail are especially important for climbing and balancing on twigs and grass stems. Some species have a nail rather than a claw on digit 5 of the hindfoot, and tend to be more terrestrial than others (Ziekur 2006). The mammary formula is 2 – 2 = 8.

The skull is small with a round braincase, a narrow rostrum, and a narrow and vertical zygomatic plate carrying a distinct masseteric knob at its lower anterior corner. Incisive foramina extend to the middle row of the upper M1. Upper incisors are small, orthodont, each with a single longitudinal groove. Cheek teeth are rather narrow; M2 is about half the size of M1; M3 is minute; cusps of M1 are biserial (two cusps in each row), with additional small lingual cusps on a middle lamella of M1; on M2 additional cusps are expressed less or absent. The morphology of the skull and the dentition are very uniform in the genus but the pelage shows great variabiliy in colour and marking. Differences in skull length usually are very small, and measurements often overlap broadly. Classification of the species is therefore often based on rather few details (Heim de Balsac & Lamotte 1958; Dieterlen 1971).

The distributional limits of many of the currently recognized 12 species (including 44 synonyms) of *Dendromus* are unresolved, and karyological information is missing for most species. The genus therefore is in need of further study and revision. As concerns systematics, it is one of the most difficult genera of African rodents. Earlier, the Dendromurinae were classified as a subfamily of the Muridae (e. g. Thomas 1896; Simpson 1945; Musser & Carleton 1993). Carleton & Musser (1984) already questioned this systematic position. Results of DNA hybridisation and mitochondrial and nuclear gene sequence studies finally supplied the basis for grouping the Dendromurinae together with five further subfamilies in the family Nesomyidae within Muroidea (Musser & Carleton 2005).

In this study, new specimens from the Imatong Mountains in Southern Sudan are described as a new species. The sample is compared with the related *Dendromus mystacalis* from Ethiopia and with several forms from East and Central Africa currently assigned to that species.

2. MATERIAL AND METHODS

The present paper continues my revisionary studies of the rodent fauna of the Sudanese Republic (DIETERLEN & RUPP 1978; HUTTERER & DIETERLEN 1981; DIETERLEN & NIKOLAUS 1985). The research is mainly based on collections obtained by Hans Rupp (†1979) and Gerhard Nikolaus in Ethiopia and Sudan between 1971 and 1983. Almost all the rodent material is housed in the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS). Comparative material was studied in the following museum collections: Museum of Comparative Zoology (MCZ), Harvard University, Cambridge (Mass.), U.S.A.; Zoological Museum of the University of Copenhagen (ZMUC), Denmark; British Museum (Natural History), London, U.K.; Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), Germany. In addition to the relevant literature, the author's fieldwork and taxonomic studies of several species of *Dendromus* in the Congolese Kivu Highland (Albertine Rift Valley) served for comparison (DIETERLEN 1969, 1971, 1976).

3. RESULTS

3.1. Species of *Dendromus* in the Sudan Republic

Only two species were recorded from the territory of the Sudan Republic so far: *D. mystacalis* by SETZER (1956), and *D. messorius* by MUSSER & CARLETON (2005). A record of *D. mesomelas* subspec. (SETZER 1956) was based on an incorrect determination. Most of the 17 specimens of *D. mystacalis* preserved in museum collections were collected by J. S. OWEN and H. HOOGSTRAAL. A third (new) species, to be described below, was collected by J. S. OWEN, H. RUPP, and G. NIKOLAUS.

Dendromus mystacalis lineatus Heller, 1911

Material from South Sudan (17). All nine localities are in the Equatoria Province, seven of them E of the Bahr el Jebel (White Nile) and S of Torit (Fig. 1): Issore (40 miles S of Torit), ZMUC 1753; Katire, ZMUC 14051, 14125;

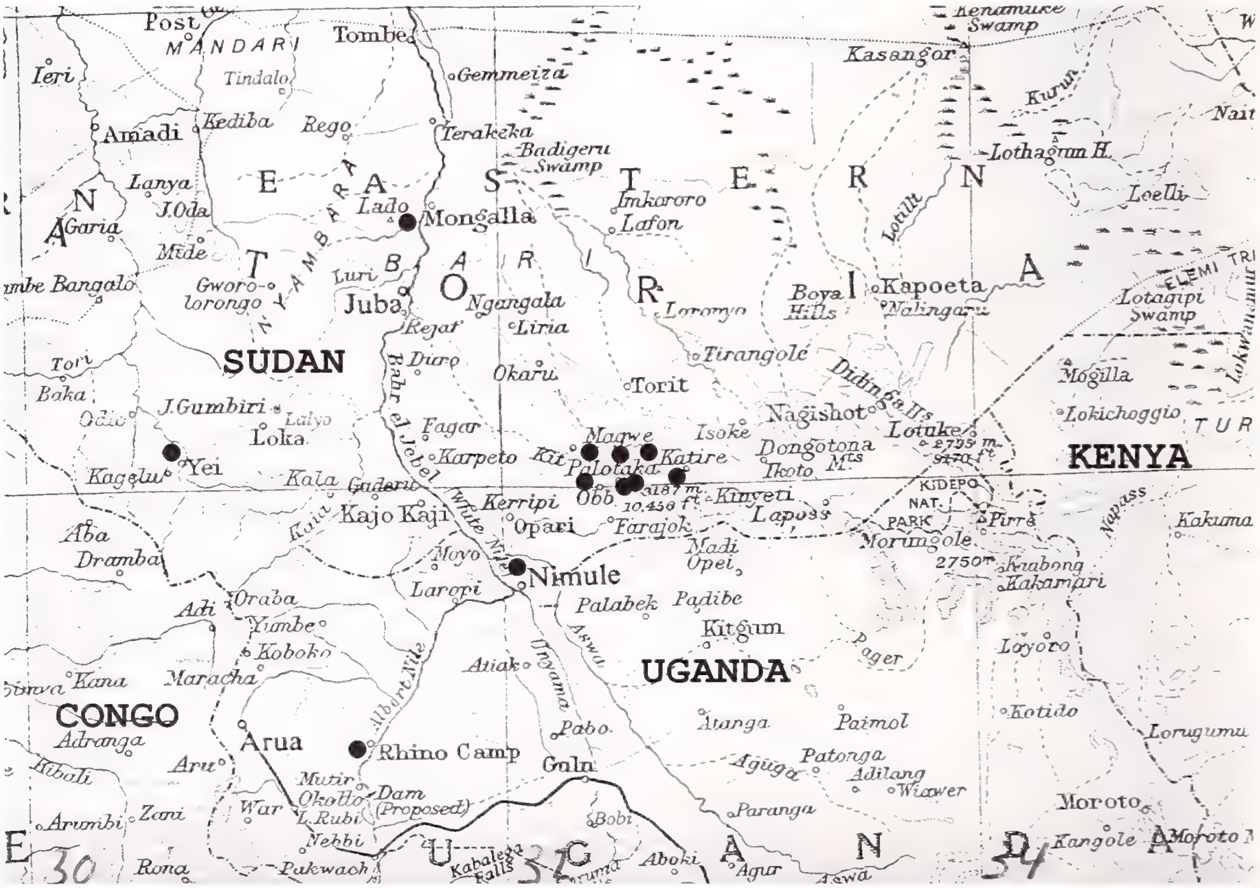
Post
MANDARI
Tombe
Ieri
Tindalo
Gemmeiza
Kasangor
Swamp
Kuruk
Nait
Amadi
Kediba
Rego
Terakeka
Badigeru Swamp
Lothagum H.
Lanya
E
A
S
T
E
R
N
J.Oda
Lado
Mongalla
Imkororo
Lafon
Loelli
Agaria
Mide
Lotilla
Gworo-lorongo
Luri
B
A
R
Boya Hills
Kapoeta
Nalingaru
A
ELEMI TRI.
Lotagipi Swamp
umbe Bangalo
Juba
O
Ngangala
Lorromyo
Rejaf
Liria
SUDAN
Diiro
Okaru
Tirangole
Didinga Hills
Mogilla
Lokwanamur
Tori
Baka
Bahr el Jebel
Torit
Nagishot
Lotuke
Lokichoggio
TUR
J.Gumbiri
Lalyo
Loka
Fagar
Magwe
Isoke
Dongotona Mts
2795 m 9170 ft
KENYA
Yei
Karpeto
Kit
Katire
Kagelu
Kala
Gaderu
Palotaka
Ikoto
KIDEPO NAT. PARK
Obb
3187 m 10,456 ft
Kinyeti
Napass
Kakuma
Aba
Kajo Kaji
Kerripi
Opari
Faraiok
Laposs
Pirre
Dramba
Moyo
Madi Opei
Morungole
2750 m
Kaabong
Kakamari
Nimule
Adi
Oraba
Laropi
Palabek
Padibe
Yimbe
Koboko
Kitgum
Pager
Loyoro
Kana
Maracha
Atiak
Aswa
Unyama
UGANDA
CONGO
Albert Nile
Adranga
Arua
Rhino Camp
Pabo
Atanga
Paimol
Kotido
Lorugumu
Aru
Gulu
Aguga
Patonga
Adilang
Wiawer
Kibali
Mutir
Okollo
Dam (Proposed)
Moroto
Arumbi
Zani
War
L.Rubi
Bobi
Paranga
Nebbi
Kangole
Moroto
E
30
Rona
Pakwach
Kabalega Falls
32
G
Karuma
Aboki
A
Agur
N
Aswa
D
34
A

Fig. 1. Distribution of *Dendromus mystacalis lineatus* in southern Sudan and northern Uganda. The region S of Torit shows seven collecting localities, the easternmost of which, Gilo, is also the type locality of *Dendromus ruppi* n. sp.

Laboni (45 miles S of Torit), ZMUC 1852; Loa (20 miles N of Nimule), MCZ 44790; Lokwi, FMNH 79936 and four further specimens; Magwe, ZMUC 14122; Obbo, FMNH67071, 67078, 98957, USNM 67072, 67073 (not seen). Two localities from W of the Bahr el Jebel: Lado (N of Juba, 5°06'), FMNH 43482, 43483; Yei, FMNH 85382 (possibly *D. messorius*).

Remarks. The following notes refer only to populations outside of Ethiopia, from where the 'typical' species was described by Heuglin (1863). The description of the species by Bohmann (1942) was essentially correct, e. g. greatest length of skull GRLE) 19–21 mm, upper molar row (M1–M3) 3.0–3.2 mm; D 5 on hind foot always with a claw.

The geographical form closest to Sudan is *D. mystacalis lineatus*, described from Rhino Camp, on the White Nile in N Uganda. According to Bohmann (1942) its distribution extends over S Sudan, N and W Uganda and from there to the Kivu Highland. For the Ituri region, this distribution was confirmed by Hatt (1940), and for the Kivu region by Dieterlen (1971) and Verschuren et al. (1983). The form *D. acraeus* Wroughton, 1909 (type locality: Mt. Elgon, Kenya) is problematic. Studies of *D. mystacalis* from Kenya and Uganda by Dieterlen (unpubl.) show that *acraeus* (Wroughton 1909) can hardly be distinguished from *lineatus*.

Bohmann (1942) considered *acraeus* as a distinct form but included it in the species *D. ruddi*. Wroughton (1909) wrote: "Typus *acraeus* and Typus *ruddi* belong to a sample in which *acraeus* represents the extreme with dark dorsal stripe, and *ruddi* the extreme without dorsal stripe." Recently *ruddi* was included as a synonym in *D. messorius* (Musser & Carleton 2005), a species mostly without a dorsal stripe. The type series (USNM) of *D. mystacalis lineatus* from Rhino Camp includes a specimen without a dorsal stripe, and in samples of *acraeus* it may also be missing, i.e. it seems that in both forms specimens without a dorsal stripe occur. In several other species of *Dendromus* the expression of the dorsal stripe can vary, from a complete stripe to no stripe at all. Because the ranges of *D. mystacalis* and *D. messorius* overlap, misidentifications may occur.

Description of *D. m. lineatus*. Dorsally brownish or reddish-brown. The hairs of the ventral side are white or whitish down to the root. The apical parts have sometimes a yellowish tinge. Setzer's (1956) description of the dor-

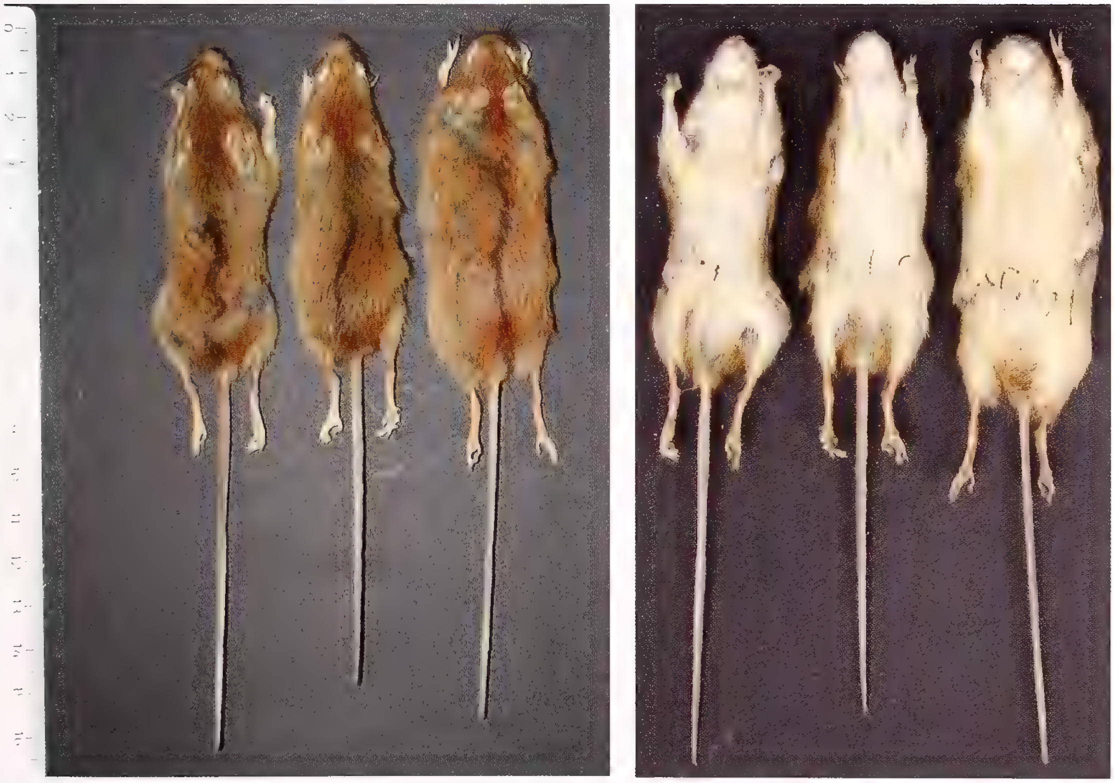

Fig. 2. Three skins of *Dendromus mystacalis lineatus* (SMNS 14737, 14738, 14736) in dorsal and ventral view. The dark mid-dorsal stripe is mostly complete, and the underparts are whitish.

Table 1. Table 1. Comparison of body and skull measurements of adult *D. mystacalis* from different regions in NE, E, and S Africa: Ethiopia and Sudan (DIETERLEN unpubl.); Kivu, Congo (DIETERLEN 1971); E Africa (Kenya und Uganda, localities Kaimosi, Sirgoit and Rhino Camp, forms *whytei, ruddi, acraeus, lineatus*) after HOLLISTER (1919); South Africa after DE GRAAF (1981); Africa (without Ethiopia) complete data of specimens given by BOHMANN (1942) under the name *D. pumilio* (now a synonym of *D. mystacalis*). HOLLISTER (1919) used as skull length only the condylo-occipital-measure (* in Table 1) which is almost exactly 10% shorter than the greatest skull length (occipito-nasal-length), here correspondingly converted. Skull measurements: GRLE, greatest length; M1–M3, length of upper molar row; INT, interorbital breadth; BRC–W, greatest width of braincase. RTL = relative tail length.

Region	HB	T	RTL	HF	EL	WT	GRLE	M1–M3	INT	BRC–W
Ethiopia	66.4	93.4	141%	17.3	13.7	–	21.52	3.35	3.23	9.79
	58–76	84–108		16–20	11–18		20.3–22.6	3.13–3.60	3.09–3.40	9.37–10.0
	n 10	n 10		n 10	n 9		n 6	n 7	n 6	n 5
Sudan	60	82	137%	17.2	11.9	–	19.6	3.14	–	–
	53–68	72–91		16–18	11–14		18.7–20.7	2.84–3.31		
	n 11	n 11		n 10	n 7		n 8	n 4		
DR Congo Kivu	63.6	77.5	122%	16.5	12.8	8.1	20.0	3.15	2.8	9.25
	53–73	63–83		16–18.5		4–12	18.8–21.3	3.0–3.5	2.6–3.4	8.9–9.6
	n 18	n 18		n 18		n 18	n 11	n 11	n 11	n 11
East Africa	63.7	82.4	129%	–	–	–	19.25 *	3.03	2.9	9.17
	55–70	71–100					17.5–21.1	2.8–3.3	2.5–3.3	8.4–9.8
	n 29	n 29					n 29	n 28	n 29	n 26
South Africa	63.5	85	134%	16.5	14	8.2	–	–	–	–
	54–80	74–103		15–20	12–16	6–14				
	n 34	n 34		n 33	n 27	n 17				
Africa	–	–	–	–	–	–	19.4	3.10	2.87	9.33
							17.6–21.6	2.8–3.4	2.5–3.5	8.7–10.0
							n 47	n 48	n 71	n 66

sal stripe of eight specimens from South Sudan is correct: „The type specimen of *D. p. lineatus* has a pronounced mid-dorsal black stripe. None of the specimens in the present series shows this intense black stripe, but all agree with the remainder of the type series of *lineatus* in showing only a faint suggestion of this marking. It is quite apparent that Heller selected the most strikingly marked specimen, rather than an average one, to name as the type". Most skins of the 17 *D. mystacalis* from South Sudan have the mid-dorsal stripe poorly developed and thus confirm SETZER'S description (Fig. 2). In three specimens the stripe is absent. In samples of Ugandan *lineatus* some specimens lack a dorsal stripe, but the dorsal colouration is exactly as in typical specimens.

Body and skull measurements. Measurements of body and skull (Table 1) show that the Sudanese specimens agree very well in size with other populations of *D. m. lineatus* and also with other forms of *D. mystacalis*. With the exception of the Ethiopian sample, all (so-called) *mystacalis* agree very well in size, appearance and characteristics of skull and dentition (Figs. 3, 4; see also DIETERLEN 1971; DIETERLEN & RUPP 1978).

Altitudinal distribution. *D. mystacalis* (except for the Ethiopian form) can be characterized as an inhabitant of the Afrotropical moist savannah, preferring relative open grassy (dry and moist) biotopes. The altitudinal range of their habitats in S Sudan and N Uganda varies between 500 and 1000 m; the northernmost occurrence seems to be limited roughly by the 1400 mm-isohyete of annual precipitation. KINGDON (1974) wrote "It is a low altitude species and is not found much above 2000 m". This may be true for many regions, but not everywhere. In Ethiopia (typical region of *D. mystacalis*) the distribution ranges from 1200 to 3800 m, predominantly between 2000 and 3000 m NE and E Congo: Garamba NP 700–1000 m (MISONNE 1963; VERHEYEN & VERSCHUREN 1966); Ishango, Virunga NP 950 m (VERHEYEN al. 1983); Lwiro (Kivu Highland) ca. 1500–2000 m (DIETERLEN 1971, 1976). Kenya: Taita Hills ca. 1800 m, Kaimosi ca. 1800 m (HOLLISTER 1919). Tanzania: Oldeani ca. 2000–3000 m (DIETERLEN unpubl.). Malawi: Nyika Plateau ca. 2150 m (ANSELL & DOWSETT 1988). Southern Africa (incl. Zimbabwe, Zambia, Mozambique): DE GRAAF (1981; SKINNER & SMITHERS 1990).

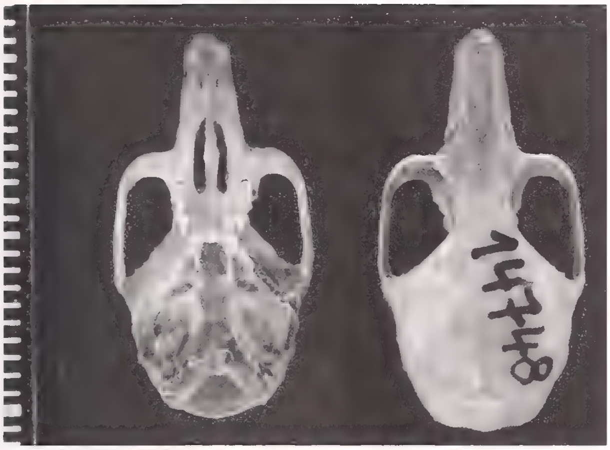

Fig. 3. Skull of a large adult *Dendromus mystacalis lineatus* (SMNS 14748; greatest length of skull 21.17 mm) from the Kivu area, D. R. Congo. Note the rounded braincase, strong interorbital region, almost squarish zygomatic arches, and long incisive foramina.

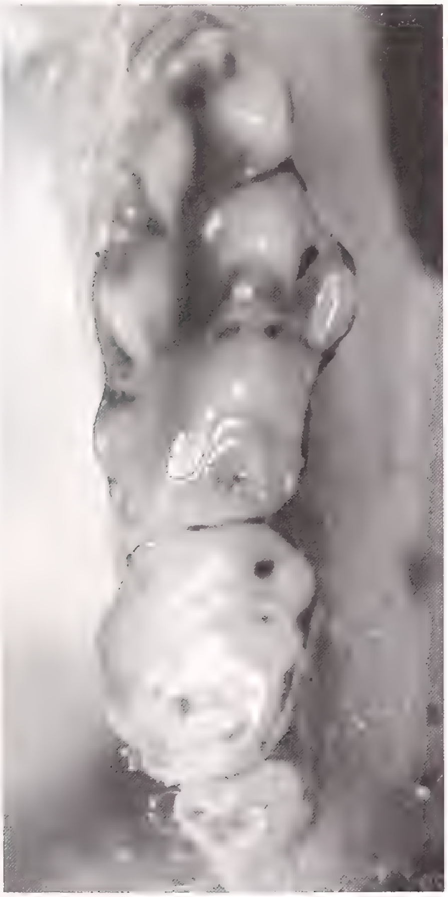

Fig. 4. Upper right molars of *Dendromus mystacalis lineatus* (SMNS 14750). Note the large M1 with biserial cusps and a longitudinal valley, separating the labial t3, t6, t9 from the lingual "t0", t2, t5, and t8. A "t4" is lingually attached to t5; the cusp pattern on M2 is still visible but heavily worn; M3 very small, as typical for the genus.

Habitat. In Ethiopia the species is "nearly always associated with long grass and bushes" (Yalden et al. 1976; Rupp 1980). NE Congo, Garamba NP: dry savannah, but found there in moist habitats around swamps etc. (Verheyen & Verschuren 1966). Congo (Kivu Highland): moist savannah, but only in relative dry grassy habitat mixed with bush vegetation, possibly due to competition with two other species of *Dendromus* (Dieterlen 1971). N Kivu: «biotope caractéristique, végétation élevée, broussailleuse, que l'on trouve sur les bords des marais nombreux qui occupent les fonds de toutes les vallées» (Misonne 1963). E Africa: "*D. mystacalis*… has adapted to cultivation quite readily …" (Kingdon 1974). Southern Africa: grassland associated with rank vegetation, especially stands of high coarse grasses such as *Hyparrhenia* sp. at 1–2 m height (De Graaf (1981; Skinner & Smithers 1990).

Nest. "This is the species to which the only positive tree-dwelling records are attached, but the habitats of the different forms and apparently of the same form in different locations, are variable" (Rosevear 1969, on *D. mystacalis*). For East Africa Kingdon (1974) noted, ".. it is not unusual to find nests in garden shrubs, banana trees and banana bunches, in sweet potato vines, pineapples, palms and in thatched roofs. Their nests may be three metres or more from the ground but are generally lower down in thick herbaceous vegetation." Owen (1953) provided the following information on nest sites for Sudanese records of *D. mystacalis*: "in tree, in banana garden, under stone, swamp near river, tree near river." The species is certainly more common than the small number of specimens in museum collections may suggest, probably because of its small size and weight (10 g). Moreover, because of its climbing habits it comes down to the ground where traps are placed only occasionally (Dieterlen 1971).

Dendromus sp.

An almost unbelievable observation was reported by Heuglin & Fitzinger (1866) and Heuglin (1877) but never cited in the scientific literature: Heuglin collected specimens of *Dendromus* on the Nile island Argo near Dongola (19.13 N, 30.27 E) in N Sudan, that is, in the middle of the Nubian desert.

The original text (in German) of Heuglin & Fitzinger (1866) reads: "Anmerkung. Aus dieser Gattung kommen in Nubien, Ost-Sudan und Abyssinien verschiedene Arten vor. Leider sind Heuglin die beiden auf der Insel Argo bei Dongola und im Belegas-Thale in Abyssinien von ihm eingesammelten in Verlust geraten, bevor er dieselben genau untersuchen und die Art bestimmen konnte." Heuglin (1877) wrote: „Bisher kannte man nur südafrikanische Vertreter der Gattung der Baummäuse *(Dendromys)*. Mir ist es gelungen, mehrere hierher gehörige Arten in Nordostafrika aufzufinden. Leider sind mehrere der gesammelten Exemplare in Verlust gerathen, namentlich einige, welche wir in Vogelnestern auf der Insel Argo bei Dongolah erbeuteten, andere im Belegas-Thal...“. In brief, he collected several *Dendromus* in bird nests on the island of Argo but the specimens were unfortunately lost before they could be studied properly. HEUGLIN'S (1863) descriptions of two forms from Ethiopia, *D. mystacalis* and *D. pallidus* (now a synonym of *D. melanotis*), is good proof that he perfectly knew these rodents. Therefore there is no reason to question that his specimens from Argo Island were members of the genus *Dendromus*. HEUGLIN'S (1877) report suggests that he himself participated in the capture of the animals.

I became aware of this bibliographic record rather late, around 1995, but had already earlier (DIETERLEN 1971, p. 130) expressed the assumption that specimens of *Dendromus* could have existed along the White Nile in S Sudan during times of a more favourable climate. It is common notion now that *Dendromus* (and other animals) had the opportunity to disperse from the Upper Nile region in Uganda northwards as early as 10.000 yrs B.P., when the tropical rain forest began to extend northwards, along with the connected savannah belt. During that period the White Nile gained its role as a large river with an enormous climatical influence, as it has today (see KENDALL 1969; LIVINGSTONE 1975; HAMILTON 1982). In the absence of fossil evidence or recent records that could document a northward dispersion, we can however presume that abundant dry or moist grasland habitat suitable for species of *Dendromus* existed in the Bahr-el-Ghazal region.

It is not known whether *Dendromus* still exists on Argo Island. How did these animals reach that remote place? One possibility is by natural dispersal during a longer favourable (moist) Quaternary period (ca. 8000–3000 B.P.; see LIVINGSTONE 1975) in the Sahara. Then its historical occurrence on Argo Island would have been extremely isolated. An alternative would be a displacement on a ship during historical times along the White Nile (by more than 2000 km), or from the Ethiopian Highlands or the lower parts of the Blue Nile valley, or downstream the Atbara River.

Dendromus melanotis (A. Smith, 1834)

Not recorded from Sudan, but the presence of *D. melanotis spectabilis* Heller, 1911 cannot be excluded because it occurs at Rhino Camp, Uganda, just about 100 km away from the Sudanese border. The forms s*pectabilis* and *nigrifrons* True, 1892 are probably closely related and are both treated as synonyms of *D. melanotis* by MUSSER & CARLETON (2005).

Dendromus messorius (Thomas, 1903)

Distributed in W Africa (Ghana to Cameroun), D. R. Congo, Uganda and Kenya. MUSSER & CARLETON (2005) recorded specimens from S Sudan, two from Torit (USNM 299 833–834), and another specimen from the former locality Gondokoro in the region of Juba. The form *ruddi* Wroughton, 1910 is known from Rhino Camp, Uganda. *Dendromus messorius* prefers moist habitats and was mostly recorded from open areas close to rain forest (HATT 1940; DIETERLEN 1971). The species can be confounded with *D. mystacalis* because of its white belly and the frequent absence of a mid-dorsal stripe. Both species may occur sympatrically (HATT 1940).

Dendromus ruppi n. sp. (Figs 5, 6, 7)

Dendromus mesomelas subsp.: Setzer 1956

Holotype. SMNS 27 572, skin (mounted on cardboard) and skull of adult female; field number 447; collected 23 April 1978 by Hans Rupp. Condition of skin and skull good. Standard measurements (in mm): Head and body length 74 mm, tail 112 mm, hindfoot 19 mm, ear 15 mm, weight 10 g.

Paratypes (17). ZMUC 10805, Gilo/ Sudan, leg. J. S. Owen; ZMUC 14121, Gilo, leg. J .S. Owen; ZMUC 14124, Gilo, leg. J. S. Owen; ZMUC uncatalogued, field no. 978, Gilo, leg J. S. Owen; MCZ 45256, Gilo, leg. J. S. Owen; MCZ 45265, Gilo, leg. J. S. Owen; SMNS 27235, Gilo, leg. G. Nikolaus, field no. 386; SMNS 27236, Gilo, leg. G. Nikolaus, field no 387; SMNS 27570, Gilo, leg. H. Rupp, field no. 388; SMNS 27571, Gilo, leg. H. Rupp, field no. 408; SMNS 27572, Gilo, leg. H. Rupp, field no. 447; SMNS 27573, Gilo, leg. H. Rupp, field no. 508; SMNS 27574, Gilo, leg. H. Rupp, field no. 540; SMNS 27575, Gilo, leg. H. Rupp, field no. 541; SMNS 30086 Gilo, leg. G. Nikolaus, field no. 1503; SMNS 30087, Gilo, leg. G. Nikolaus, field no. 1518; SMNS 30088 Gilo, leg. G. Nikolaus, field no. 1519.

Type locality. Gilo, Imatong Mts., East Equatoria, South Sudan; altitude ca. 1800–1900 m. Two habitats were noted by Rupp and Nikolaus: “near the potato farm” and “in grassy biotopes around a swamp”.

Diagnosis. A species of *Dendromus* resembling *D. mystacalis*, but clearly larger in head and body length and in

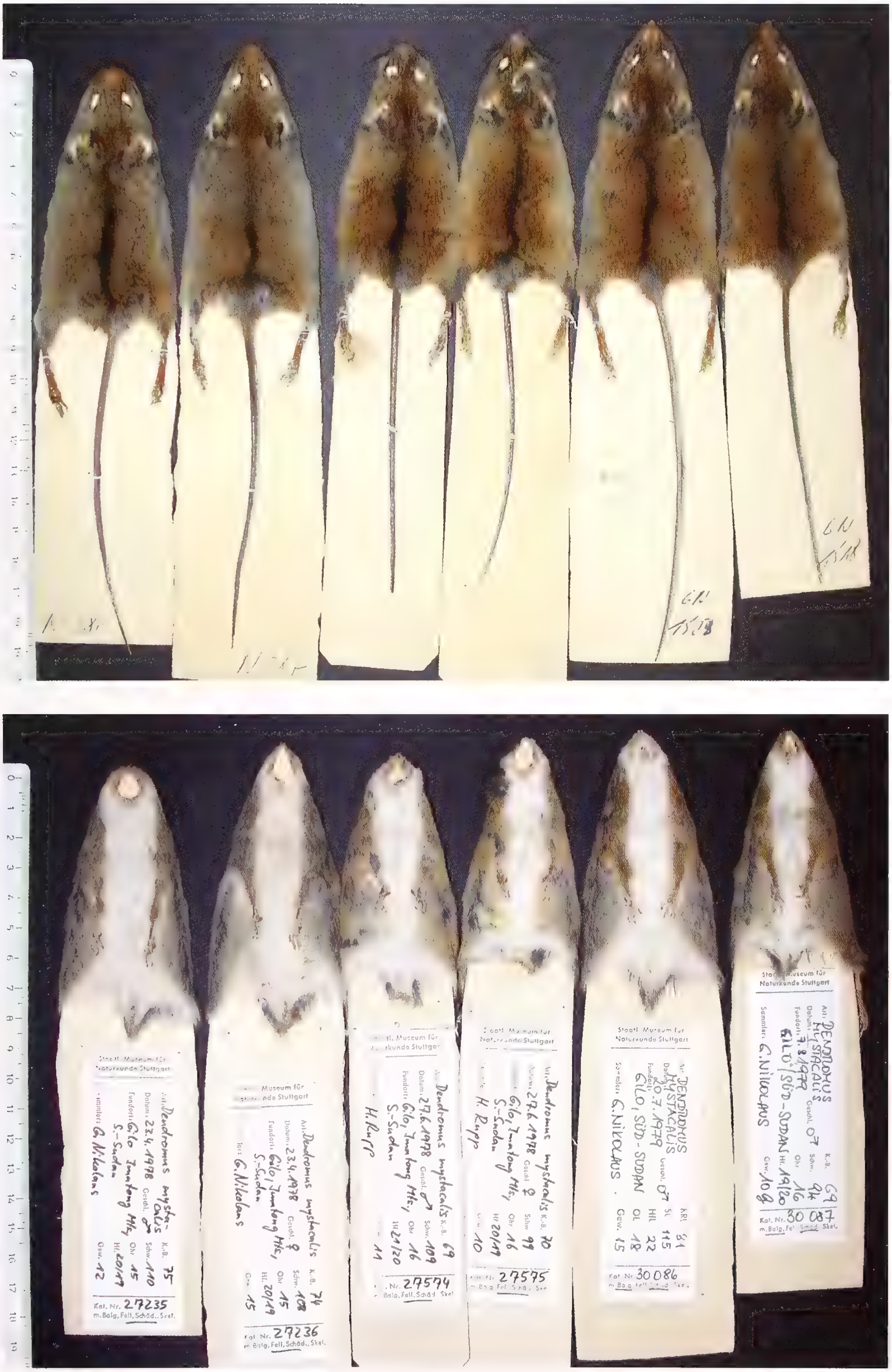
Kat. Nr. 27235
Kat. Nr. 27236
Kat. Nr. 27574
Kat. Nr. 27575
Kat. Nr. 30086
Kat. Nr. 30087

Fig. 5. Skins of 6 specimens of *Dendromus ruppi* n. sp. in dorsal and ventral view. From left to right: SMNS 27235, 27236, 27574, 27575, 30086, 30087 (all paratypes).

Table 2. Body and skull measurements of the specimens of *Dendromus ruppi* n. sp. collected in the area of Gilo.

Mus.	No.	age	HB	TL	HFL	EL	WT (g)	GRLE	M1–M3	INT	BRC–W
ZMUC	10805	–	82	91	20	14	–	–	–	–	–
ZMUC	14124	–	74	104	20	13					
ZMUC	14121	–	79	106	20	17	–	c. 22.5	–	–	–
ZMUC	(978)	–	77	95	20	13	–	–	–	–	–
MCZ	45256	2	69	98	18	14	–	22.1	–	–	–
MCZ	45265	3	76	107	19	13	–	c. 23.0	–	–	–
SMNS	27235	3	75	110	20	15	12	23.3	3.63	3.4	11.0
SMNS	27236	2	74	108	20	15	15	22.1	3.53	3.3	10.7
SMNS	27570	–	72	98	19	15	11	–	–	–	–
SMNS	27571	5	74	110	19	14	10	–	3.38	–	–
SMNS	27572	3	74	112	19	15	10	22.4	3.47	3.4	10.3
SMNS	27573	–	63	98	19	14	8	–	3.56	–	–
SMNS	27574	4	69	109	21	16	11	–	3.54	–	–
SMNS	27575	3	70	99	20	16	10	–	3.64	–	–
SMNS	30086	2	81	115	22	18	15	23.9	3.61	3.5	11.1
SMNS	30087	2	69	94	20	16	10	22.4	3.50	3.3	10.1

absolute tail length: *D. mystacalis* 82.0 mm (Sudan), 93.4 mm (Ethiopia) vs. *D. ruppi* 103.4 mm. Underparts purely white, median dark stripe on dorsum and head present in all specimens studied. A tuft of white hairs is present at the ear basis.

Distribution. At present only known from the region of Gilo in the Imatong Mountains, Sudan.

Description. A small *Dendromus* resembling *D. mystacalis*, but clearly larger and with a much longer tail (Fig. 5). Characterized by white underparts, the hairs white from base to tip. Underparts well delimited from the typical brownish pelage on head and dorsum. The blackish middorsal stripe is variable in length but never absent; normally extending from the neck back to the middle dorsum or even to the base of the tail; forward from the neck the stripe (the colour now changes to dark brown) may reach

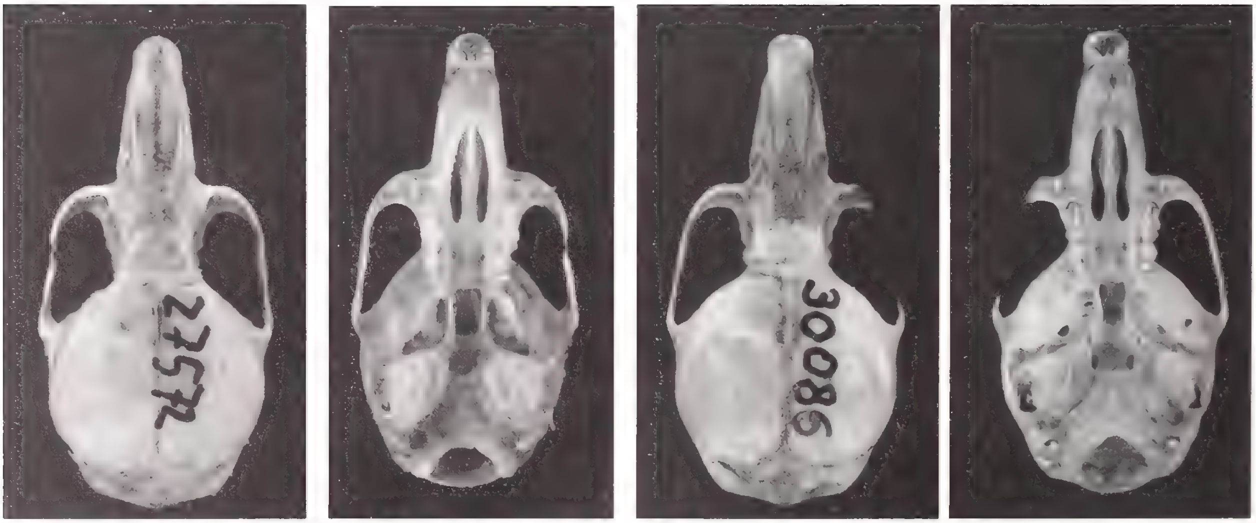

Fig. 6. Two skulls of *Dendromus ruppi* n. sp.in dorsal and ventral view. Left, SMNS 27572 (holotype), a specimen of medium size (22.4 mm); right, SMNS 30086, the largest specimen (23.9 mm). Note the well rounded braincase and the shape of the zygomatic arches compared to *D. mystacalis* (Fig. 3).

Table 3. A comparison of body and skull measurements of *Dendromus ruppi* n. sp., *D. mystacalis* from the South Sudanese lowland, and the Ethiopian *D. mystacalis*. Mean, range, and sample size given. RTL = relative tail length.

Species	HB	TL	RTL	HFL	EL	WT (g)	GRLE	M1–M3	INT	BRC–W
D. ruppi (Gilo)	**73.6** 63–82 n 16	**103.4** 91–115 n 16	**140%**	**19.8** 18–22 n 16	**14.8** 13–18 n 16	**11.2** 8–15 n 10	**22.7** 22.1–23.9 n 8	**3.54** 3.38–3.64 n 9	**3.38** 3.3–3.5 n 5	**10.62** 10.0–11.1 n 5
D. mystacalis (Sudan)	**60** 53–68 n 11	**82** 72–91 n 11	**137%**	**17.2** 16–18 n 10	**11.9** 11–14 n 7	–	**19.6** 18.7–20.7 n 8	**3.14** 2.84–3.31 n 4	–	–
D. mystacalis (Ethiopia)	**66.4** 58–76 n 10	**93.4** 84–108 n 10	**141%**	**17.3** 16–20 n 10	**13.7** 11–18 n 9	–	**21.52** 20.3–22.6 n 6	**3.35** 3.13–3.63 n 7	**3.23** 3.09–3.40 n 6	**9.79** 9.37–10.50 n 5

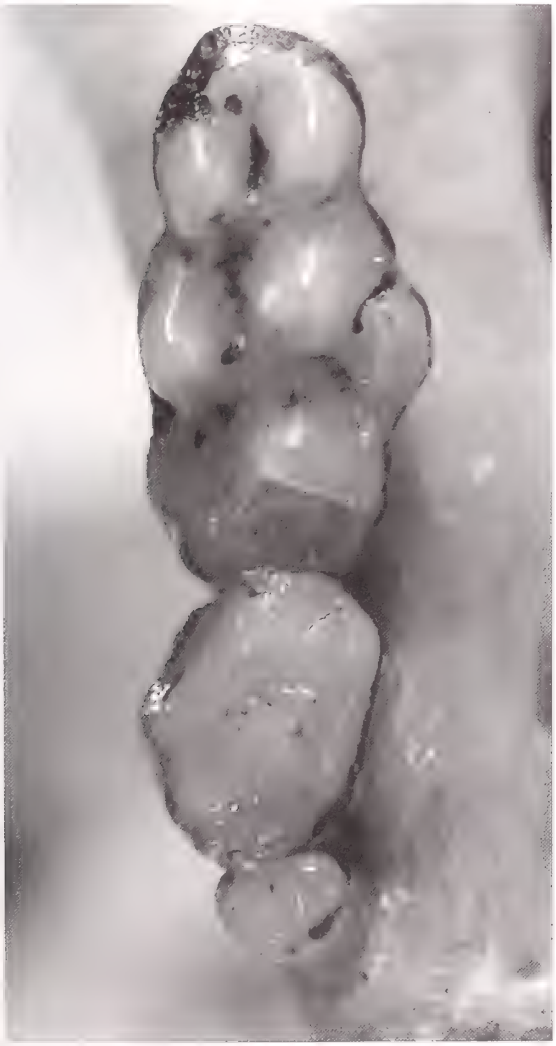

Fig. 7. Upper right molars of *Dendromus ruppi* n. sp. (SMNS 30086). Cusp pattern on M2 starting to wear down; M3 typically small.

its end between the eyes. A black hair spot on the heels, as typical for the genus. The hind feet are reddish brown. The short hairs on the ears are also reddish brown. There is a small but distinct spot of white hairs at the base of the ears. The upper side of the tail is pigmented dark but bears short light bristles. Mammary formula 2 – 2 = 8. D 5 of hind foot bearing a short claw.

The skull (Fig. 6) has the typical characteristics of the genus: rounded braincase, narrow zygomatic plate and a distinct masseteric knob at its lower anterior corner. Anterior edge of supraorbital bow smooth (not chambered). Upper incisors longitudinally grooved. M1-length about 57% of upper molar row, M2 ca. 35%, M3 minute. Molars (Fig. 7) rather narrow, breadth of M1, M2, M3 clearly larger than in *mystacalis* (see below). The posterior part of M1 behind its prominent t8 relatively broad in appearance (but similar to the same area of *D. mystacalis*). In most specimens t9 is worn down on the labial side and appears crater-like.

Measurements. Tables 2, 3.

Ecological and biological data. Three out of seven specimens in the SMNS were collected in a swamp near Gilo at c.1800 m, and four in the area of the (so-called) "potato farm" above Gilo (c.1900 m). The two MCZ specimens came from a "nest in olive tree" (Setzer 1956). The SMNS sample comprises six males and five females, collected between April 1978 and August 1979. A female caught in April 1978 had four embryos (13 mm in diameter); four males caught between April and July had testicle diameters of 3, 5, 5, and 6 mm, respectively.

Comparisons. *Dendromus mystacalis lineatus* in Sudan is a lowland species, with its highest altitudinal record in Katire at c. 1000 m, on the foothills of the Imatong Mts.

Table 4. Measurements of body and skull of *D. mystacalis* from Ethiopia. Age class 1 sem.-young adult, 2 young adult, 3 adult, 4 adult/old adult, 5 old adult.

Coll.No.	age class	HB	T	HF	E	WT (g)	GRLE	M1–M3	INT	BRC–W
BMNH 28.1.11.143	3	71	87	18	13	–	21.71	3.60	3.19	9.37
BMNH 128.1.11.144		–	61	94	18	15	–	–	–	–
BMNH 28.1.11.145	3	67	84	17	18	–	21.53	3.30	3.09	9.70
BMNH 28.1.11.146	1	58	89	16	14	–	20.27	3.24	3.17	–
BMNH 1934.2.24.88	–	58	87	16	13	–	–	–	–	–
BMNH 59.660	–	65	95	16	13	–	–	–	–	–
BMNH 70.655	4	76	105	17	12	–	22.31	3.42	3.40	9.78
BMNH 70.656	2	64	96	16	11	–	20.68	3.13	3.24	9.63
SMNS 23720	2	71	108	19.5	–	13	–	3.43	–	–
SMNS 23732	4	73	89	18	14	–	22.61	3.33	3.28	10.50
Mean	–	**66.4**	**93.4**	**17.3**	**13.7**	–	**21.52**	**3.35**	**3.23**	**9.79**
range		58–76	84–108	16–20	11–18		20.3–22.6	3.1–3.6	3.1–3.4	9.4–10.5
n		n 10	n 10	n 10	n 9		n 6	n 7	n 6	n 5

Other populations (outside Ethiopia) are also known from lower altitudes (BOHMANN 1942; DIETERLEN 1971; KINGDON 1974; ANSELL & DOWSETT 1988). The typical *D. mystacalis* from the Ethiopian Highlands, however, is exclusively a high mountain animal. *D. ruppi* is also a highland species, known from the Imatong Mts. at altitudes between 1800 and 1900 m. On the neighbouring Mt. Kinyetti (3187 m, the highest peak in Sudan Republic) an occurrence at even higher altitudes may be possible up to about 2500 m.

D. ruppi and (non-Ethiopian) *D. mystacalis* share the white pelage of the underside and further characters, but *D. ruppi* is considerably larger in external, cranial, and dental measurements (length of upper molar row, Table 5). The dorsum of *D. ruppi* is darker than in *D. mystacalis* and always shows a mid-dorsal stripe. There are further differences in the breadth of the molars between *D. ruppi* (n = 9) and *D. mystacalis* (n = 5). M1 from "t1" to t6: *ruppi* 1.14 mm (1.02–1.21) vs. *mystacalis* 1.02 mm (0.98–1.05). M2: *ruppi* 0.97 mm (0.86–1.04) vs. *mystacalis* 0.83 mm (0.80–0.86). M3: *ruppi* 0.49 mm (0.47–0.53), no data available for *mystacalis*.

Comments. SETZER (1956) discussed two specimens of *Dendromus* from Gilo/Imatong Mts., South Sudan, in the MCZ: "These two specimens are somewhat darker than *D. mesomelas percivali* (now a synonym of *D. insignis*, according to MUSSER & CARLETON 2005) from Mount Gargues, British East Africa. The external measurements agree rather well with *percivali*, but the skulls of the Gilo specimens, even though adult, are markedly smaller… It is apparent that these animals from the Imatong Mountains are different from any of the surrounding kinds, but owing to the broken condition of the skulls and there being only the two specimens I feel it best to identify them only at the specific level." SETZER (1956) did not know that J. S. Owen, the collector of the MCZ specimens, had already sent another four specimens from the same locality to the ZMUC at Copenhagen, which Setzer could not consider in his paper. He also failed to recognize that the specimens had entirely white underparts and therefore could not belong to *D. mesomelas*. In the latter species the hairs of the underside are brownish-grey with an always dark basis, only on the throat and in the anal region they can be whitish (BOHMANN 1942; ROSEVEAR 1969; DIETERLEN 1971). Contrary to Setzer's statement, one of the skulls of the specimens at Harvard (MCZ 45 256) was not damaged (measurements in Table 4) and the other (MCZ 45 265) had already been repaired by MCZ staff when I measured it in 1988 (Table 4). The occurrence of *D. mesomelas* (now *D. insignis*) in the mountains of South Sudan could be expected, because *D. insignis* was already known then from high altitudes of neighbouring Ethiopia, Kenya, and Uganda.

Besides the Imatong Mts., mountains neighbouring to the east (Dongotona and Didinga Mts.) could also be populated by *D. ruppi*, at least above 1800 m. For the present, however, *D. ruppi* must be regarded as a species endemic to the Imatong Mts. which became isolated as a result of climatic changes during a drier Pleistocene postglacial/pluvial phase in Equatorial Africa (Rupp 1980; Livingstone 1975).

Etymology. I dedicate this new species to my deceased friend and colleague Hans G. Rupp. Hans died on 15 June 1979 at the age of 32, after several weeks of severe illness in a hospital in Nairobi/Kenya, to where he had been transported from South Sudan. As a student of zoology at the University of Tübingen,Germany, he had begun extensive fieldwork for his doctoral thesis on rodents and their entoparasites in southern Sudan 17 months before. In the early 1970s he undertook a number of research travels to Ethiopia and published the results about systematics, distribution and ecology of Ethiopian rodents (Dieterlen & Rupp 1976, 1978; Rupp 1980).

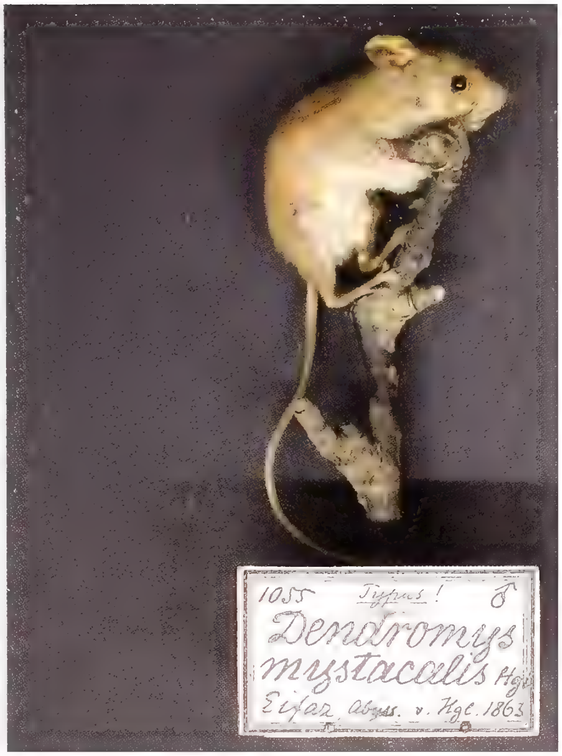

Fig. 8. Mounted holotype (SMNS 1055) of *Dendromus mystacalis* (Heuglin, 1863).

3.2. Species of *Dendromus* in Ethiopia

Four species of climbing mice are known within the territory of Ethiopia:

Dendromus mystacalis (Heuglin, 1863)

Holotype. SMNS 1055; a specimen collected by Heuglin in 1863 and sent to the *Stuttgarter Naturalienkabinett* (now SMNS) where it was registered under no. 1055 in the (Accession-) Catalogue for mammals, founded in 1837. The well-preserved specimen was mounted in a climbing posture on a short vertical branch, anchored in a wooden pedestal (Fig. 8). No skull is preserved. The inscription on the label reads: "1055 Typus! male *Dendromus mystacalis* Hgl. Eifaz, Abyss. v. Hgl. 1863". Based on its size and the measurements given by Heuglin (1863) the specimen was subadult. After 144 years of preservation the reddish-brown dorsal pelage has become dull and the (originally?) weakly developed mid-dorsal stripe disappeared. However, the blackish-grey basal part of the hairs remains unchanged. Heuglin's original description (in German) reads:

„*Oberseite und Außenseite der Füße zart rostig ockerfarben; Unterseite ein eckig nach den Zügeln einspringendes Feld, das von den Halsseiten ausgeht und bis unter und vor das Auge reicht, sowie Innentheile der Behaarung der Füße rein weiß; beide genannte Farben streng von einander geschieden; auf der Rückenmitte schwache Andeutung eines graulichen Längsstreifes. Schnurren schwärzlich; hinter der Ohrbasis ein hell ockerfarbiger Fleck; Schwanz lang, schlank, mit sehr zarten Härchen ziemlich dicht besetzt; Nasenkuppe, Nägel und Zehenballen fleischfarbig. Auge mittelgroß, hervorstehend, braun; längs der Außenseite der oberen Schneidezähne eine starke Furche. Körperlänge 2” 5’”* (= 65 mm, given in the old German measurement Zoll). *Schwanzlänge 3”* (= 75 mm). *Ohrhöhe stark 15’”* (= > 15 mm). *Das Ohr zu beiden Seiten etwas um- und eingebogen; ausgebreitet so breit als hoch. Wir erbeuteten nur ein einziges Exemplar dieser zierlichen Art, und zwar im Horst eines Raubadlers, wo das Thierchen wohl 40 Fuß über dem Boden, seine Behausung aufgeschlagen hatte. Im Magen fand sich ein grüner Pflanzenschleim. Vorkommen in der Ebene von Eifag in Central-Abessinien, auf 6000 Fuß Meereshöhe.*“

Table 5. Comparison of body and skull measurements summarized from published collections of *D. mystacalis* of Sudan (this paper); Congo (Dieterlen 1971); East Africa (Hollister 1919); South Africa (De Graaff 1981), and Africa (globally, Bohmann 1942) , and those from the highlands of Ethiopia (this paper) (Data given by Verschuren, Van der Straeten & Verheyen 1983 from Congo and Rwanda are not included but confirm the summarized measurements of Africa).

Measurement	Africa	Ethiopia
HB	**63.5 mm** (53–80) n 92	**66.4 mm** (58–76) n 10
T	**82.0 mm** (63–100) n 92	**93.4 mm** (84–108) n 10
HF	**16.6 mm** (15–20) n 61	**17.3 mm** (16–20) n 10
E	**13.0 mm** (10–17) n 52	**13.7 mm** (11–18) n 9
WT	**8.15 g** (4–14) n 35	–
GRLE	**19.5 mm** (17.5–21.6) n 88	**21.52 mm** (20.3–22.6) n 6
M1–M3	**3.10 mm** (2.8–3.5) n 91	**3.55 mm** (3.13–3.63) n 7
INT	**2.87 mm** (2.5–3.5) n 111	**3.23 mm** (3.09–3.40) n 6
BRC-W	**9.30 mm** (8.4–10.0) n 103	**9.79 mm** (9.39–10.50) n 5

Comparison of the holotype with further specimens collected. Since the type seems to have never been studied or compared, and Heuglin's description was barely consulted, a comparison with further *mystacalis* specimens from Ethiopia and other parts of Africa has probably not been undertaken. Annotations as to literature, distribution and collections can be found in the "Catalogue of the Mammals of Ethiopia" (Yalden et al. 1976, 1996) and in papers with isolated data or single unpublished records. Yet, no critical comparisons of the Ethiopian *mystacalis* with all other forms designated as *mystacalis* seems to have taken place.

Material of Ethiopian *D. mystacalis* studied. BMNH 1934.2.24.88, Bab Bar Sir, Wuha River, 3 miles N of Lake Tana, Cheeseman Collection; BMNH 59.660, Sidamo (07.00 N/ 36.30 E), coll. F. K. Allison; BMNH 70. 655, Mouth of Didessa River (10.05 N/35.38 E), coll. Great Abbai Expedition 1968; BMNH 70. 656, Junction of Nile and Guder River, Blue Nile Gorge (09.50 N/ 37.41E), same Expedition; BMNH 28.1.11.142, 28.1.11.143, 28.1.11.144, 28.1.11.145, all from Dangila, S of Lake Tana (11.17 N/ 36.56 E); BMNH 28.1.11.146, Kolaj village, Domkan River (10.42 n/36.31 E), all by Cheeseman Collection; SMNS 1055, Eifag (Eifaz) (12.03 N/37.46 E), T. von Heuglin (holotype); SMNS 23720, Chencha (06.16 N/37.40 E), H. Rupp; SMNS 23732, Dorsey (Dorse) (06.13 N/37.40 E), H. Rupp.

Description. Generally little colour variation among the forms of *D. mystacalis*. The colour of the upper parts of Ethiopian specimens is very similar compared to other forms: a brownish- or ochre-grey (also reddish tinge) over the whole back and head. Only the terminal part (2–3 mm) of the pelage hairs is coloured as described, the basal part of the dorsal hairs is uniformly dark grey. The black mid-dorsal stripe is variable (Fig. 9): in four specimens the stripe is complete from neck to root of tail, in three other specimens the stripe is thin and not visible throughout its length, and in four there is no mid-dorsal stripe at all; see also Yalden et al. (1976). No geographical variation in this character could be observed. The underside is pure white from chin to belly. Like in all species of the genus there is a dark spot of hairs just above the heels (Dieterlen 1971). The hairs of the dorsal surface of the hind foot are somewhat reddish-brown as are the short hairs on the ears. The skin of the short-bristled tail is pigmented dark on the upper side and whitish below.

Localities and altitudes (Fig. 10). Altitudes mostly as given by collectors or/and authors. Alemaya, Lake 2100 m (09.21 N, 42.01 E); Axum, S of, 2100 m (14.08 N, 38.45 E); Bab Bahr, 3 miles N Lake Tana, 1800 m (12.16 N, 37.07 E); near Boralugu, 3000 m; Chencha, 9 km N, 2700 m (06.16 N, 31.40 E); Dangila, 2000–2100 m (11.17 N, 36.56 E); Debre Tabor, 2500 m (11.50 N, 38.02 E); Didessa River (mouth), 1200 m (10.08 N, 35.38 E);

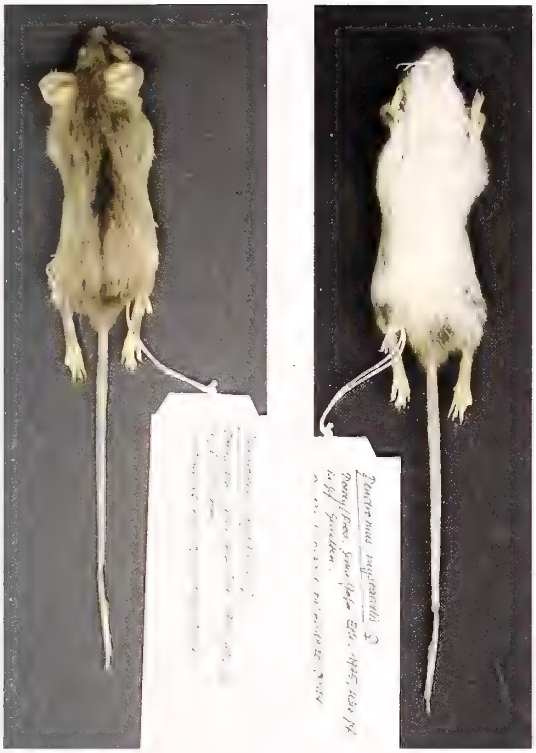

Fig. 9. Skin of a *Dendromus mystacalis* (SMNS 23732) from Ethiopia.

Didessa River (near Guma), 1900 m; Domkan (Dibken), 2000 m; Dorse (Dorsey), S, 2600–3000 m (06.13 N, 37.40 E); Eifag (Eifaz, Ifag), 2000 m (12.03 N, 37.46 E); Guder River, junction of Nile, 1800 m (09.50 N, 37.41 E); Harenna Forest, 2000 m; Katcha, S Mt. Batu, 2400 m (06.42 N, 39.44 E); Kebre Mengist, 70 km NW. 1680 m (06.23 N, 38.35 E); Kolay (Golay), Domkan River, 1600 m (10.42 N, 36.31 E); Ladjo, NW Mt. Goba, 3850 m (07.08 N, 39.33 E); Masslo, c. 40 km SW Mt. Goba (06.42 N, 39.50 E); Menagasha Forest, c. 2800 m (08.55 N, 38.37 E); Mt. Badda, W (07.50 N, 39.45 E); (Mt.) Goba, 2800 m (07.01 N, 39.59 E); Sidamo, Arussi, 2500 m (07.40 N, 39.45 E); Simien Mts. National Park, 3100–3600 m (c. 13.15 N, 37.50 E). The altitudinal distribution varies between 1200 and 3850 m, with most records between 2000 and 3000 m. The collecting localities are scattered over a vast region encompassing large parts of the western and central highlands (Yalden et al. 1976). *D. mystacalis* occurs in the vegetational zone of Woina Dega (ca. 1500–2300 m), including the (so-called) Highland Zone and the lower Montane Zone. Above Woina Dega the species ascends up to 2300–3300 m, reaching parts of the upper Montane and lower Temperate Zone (Rupp 1980).

Habitat. "This species has been recorded from a wide range of altitudes (900–3200 m) but is nearly always associated with long grass and bushes." (Yalden et al. 1976). In the Menagesha Forest, Bekele (1996) found *mystacalis* in bush vegetation (dominant plant *Carissa edulis*). Preferred habitats in the Simien Mountains National Park are Giant Heath (*Erica arborea*) forests with thick undergrowth (Müller 1977; Muhmenthaler 1999; Wehrli 1999). Notes on biotopes and nests of *D. mystacalis* are as follows: Heuglin's type came from a nest 40 ft. high in a tree with an eagle's aerie. Three specimens of the Cheeseman collection (at Dangila) were taken at considerable height in trees: "in a straw bee hive, 30 feet from ground", "same grass nest in tree in high grassland", "same tree as in…". Similar observations were made in other regions of Africa. In East Africa the species often frequents disused weaver and bishopbird nests. In the Kivu region, however, nests of *D.* cf. *mystacalis* were never found in trees, but in the absence of trees and shrubs in dry grassy biotopes with *Melinis minutiflora* and other Gramineae; nests were found between stems of grass. *D. mystacalis* was rarely seen in moist grassy biotopes (Dieterlen 1971).

Comparisons. A comparison of body and skull measurements of *D. mystacalis* samples (Tables 1, 4, 5) from various regions of Africa, but excluding Ethiopian populations, revealed surprising results. Mean values for each character (Table 5) were compared with the relatively small Ethiopian sample. In most measurements a distinct difference exists between the true Ethiopian *mystacalis* and the remaining populations, particularly in the relative tail length, length of skull, and other skull measurements.

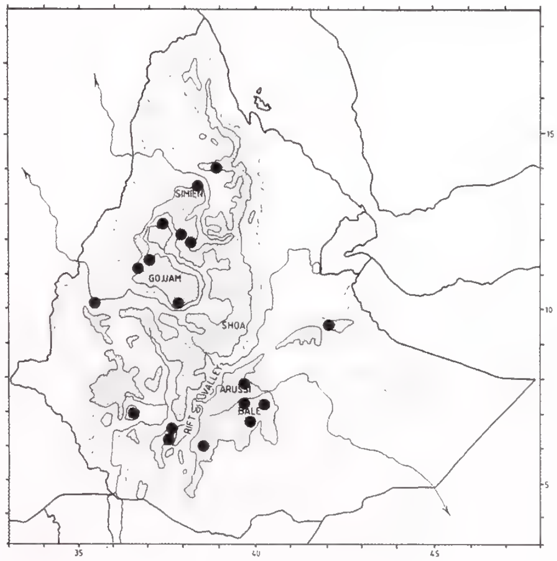

Fig. 10. Distribution of *Dendromus mystacalis* in Ethiopia.

A further difference is altitudinal distribution: Ethiopian *mystacalis* have a strictly montane distribution, while the forms which occur outside Ethiopia occur principally below 2000 m. These results question the conspecificy of all the described forms within *D. mystacalis*, an issue which should be addressed in the future, including genetic data. The description of Heuglin (1863) and the characters of the type specimen apply only to the Ethiopian populations. All the similar but clearly smaller non-Ethiopian forms, considered at present as part of D. *mystacalis*, may belong to one or more other species.The status of all the populations of *D. mystacalis* outside of Ethiopia should be reconsidered. The names *Dendromus ansorgei* Thomas & Wroughton, 1905 (Angola) and *D. jamesoni* Wroughton, 1909 (South Africa) are candidates for a possible lowland species.

Dendromus melanotis (A. Smith, 1834)

Yalden et al. (1976, 1996) listed four specimens from three localities at altitudes between 1200 and 2500 m. Another specimen (AMNH 81119) was recorded by Musser & Carleton (2005). Another three specimens not yet published were collected by H. Rupp near Chencha (2400–2700 m): two adults (SMNS 23721, 23722), one subadult (SMNS 23723). Measurements of the adults are: HB 64, 78 mm; T 85, 94 mm; HF 19, 19 mm; EL 15, 15 mm; GRLE 22.45, 22.51 mm; M1–M3 3.36, 3.51 mm; BRC–W 10.51, 11.04 mm.

No material of the form *pallidus*, described by Heuglin (1863) and listed as a synonym *melanotis* by Musser & Carleton (2005), was available for study. Heuglin wrote "*Lippengegend und die Unterseite rein weiß*" (area of the lips and underparts pure white), but without mentioning the grey basis of the white hairs, typical for *melanotis*, and without comparing it with his type specimen of *D. mystacalis*.

Dendromus insignis (Thomas, 1903)

The taxon *insignis*, formerly included in *D. mesomelas* by Bohmann (1942) and Misonne (1974), is considerably larger than the South African species *D. mesomelas*. Osgood (1936) was right to describe his record from the E slope of Mt. Albasso, Ethiopia, as *D. insignis abyssinicus*, now known by several more specimens from the highlands. Three specimens in the BMNH (72.1294, 72.1295, 76.113, leg. Largen et al. 1971) recorded from "Bale Dinshu" above 3000 m, and labeled as *D. mystacalis*, are unmistakably *D. insignis* (Dieterlen, unpubl.). Two further adult specimens from the same region were collected by H. Rupp and G. Nikolaus in 1971 and 1976 (SMNS 23724, 23983). Measurements: HB 68, 75 mm; T 103, 101 mm; HF 22/23, 21/22; EL 17, 12 mm; WT -, 10 g; GRLE -, 22.08 mm; M1–M3 3.52, 3.31 mm; BRC–W -, 10.94 mm.

Dendromus lovati (De Winton, 1899)

Endemic to Ethiopia. A distinctive small species, very different from all congeners (HB 68–90 mm, T 72–80 mm, WT 12–16 g). Not very common, at least not in trapping yields. Altitudinal distribution 2500 to 3550 m. Preferred habitats are grassland and giant heath (*Erica arborea*) forests (Yalden et al. 1976, 1996; Müller 1997; Muhmenthaler 1999).

Material studied. One specimen from Ankober (SMNS 23927). leg. G. Nikolaus.

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Zusammenfassung. Die in Äthiopien und Sudan vorkommenden Arten der Gattung *Dendromus* (Rodentia: Dendromurinae) werden revidiert. Die zu *Dendromus mystacalis* (Heuglin, 1863) gerechneten Formen der Klettermäuse aus Sudan und anderen Regionen Afrikas werden mit der typischen Population aus Äthiopien verglichen. Äthiopische *D. mystacalis* unterscheiden sich von anderen afrikanischen Populationen in ihrer Morphologie und im Lebensraum, während alle Populationen außerhalb Äthiopiens sich in Größe, Erscheinung gleichen und in ähnlichen Lebensräumen leben. Eine neue Art, *Dendromus ruppi*, wird nach Material aus den Imatong Bergen im Süd-Sudan beschrieben. Sie ist eine relativ große Bergform, die vermutlich während klimatischer Schwankungen in einer postpluvialen Phase des Pleistozäns isoliert wurde. Die neue Art ist vermutlich endemisch für die Imatong Berge.

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A large new species of *Sylvisorex* (Mammalia: Soricidae) from Nigeria and the first record of *Sylvisorex ollula* from the country

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Abstract. A new species of shrew, *Sylvisorex corbeti* n. sp., is described from SE Nigeria. The only specimen known was previously assigned to *Sylvisorex ollula*, but is considerably larger, has a longer tail, elongated hindfeet and a very large skull and thus represents the largest species of the genus. From the Obudu Mountains in SE Nigeria a new specimen is recorded which agrees well with typical *S. ollula* from lowland forest of southern Cameroon, and which represents the first species record from Nigeria.

Key words. Africa, Nigeria, Mambilla Plateau, *Sylvisorex*, new species.

1. INTRODUCTION

The shrews of Nigeria were reviewed by HUTTERER & HAPPOLD (1983) who recorded 23 species in three genera, including *Sylvisorex* Thomas, 1904, at that time known from the country only by *Sylvisorex megalura* (Jentink, 1888), a species sometimes included in the genus *Suncus* Ehrenberg, 1832 (HUTTERER 2005). HUTTERER et al. (1992) added three further species from mountain forests in SE Nigeria, *Sylvisorex camerunensis* Heim de Balsac, 1968, *Sylvisorex ollula* Thomas, 1913, and *Crocidura attila* Dollman, 1915. *Sylvisorex ollula* is the largest of the 14 species of the genus known so far (HUTTERER 2005; HUTTERER et al. 2009; MUKINZI et al. 2009). It was described from lowland forest near the River Ja in SE Cameroon (THOMAS 1904) and is known also from Gabon (BROSSET 1988; GOODMAN & HUTTERER 2004), Equatorial Guinea (LASSO et al. 1996), Central African Republic (RAY & HUTTERER 1996), Republic of Congo (QUEROUIL et al. 2003), and Democratic Republic of Congo (DIETERLEN & HEIM DE BALSAC 1979). Records from Cameroon are rare and concentrated in the south of the country (HEIM DE BALSAC 1968; GOODMAN et al. 2001). To the west, the species is known from around Mount Cameroon (HEIM DE BALSAC 1959, 1968) and from the Korup National Park (HUTTERER & SCHLITTER 1996). The record from SE Nigeria therefore appears to be isolated. However, more specimens have become available in recent years, both from Cameroon and Nigeria, and we are now in a position to re-evaluate the systematics of the populations at the north-western edge of the range of the *S. ollula* group.

2. MATERIAL AND METHODS

We studied new material from Nigeria and Cameroon obtained by G. Nikolaus and M. Barej from 1992 to 2006 (see below). These specimens are deposited in the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK); other material studied is deposited in the Estacion Biologico Donana, Sevilla (CET) and the Natural History Museum, London (BMNH). Skull measurements were taken with an electronic calliper. All measurements are given in millimetres (mm), and body mass in grams (g). The terminology of cranial and dental structures follows MEESTER (1963) and JENKINS (1984); external and cranial measurements are the same as previously defined by STANLEY et al. (2005) and KERBIS PETERHANS et al. (2008). The terminology of the skeletal elements of the limbs follows WOODMAN & MORGAN (2005). Digital X-rays were made with a Faxitron LX60 machine. The taxonomy of shrews follows HUTTERER (2005), except for the unsettled allocation of *Suncus megalura.* For the purpose of this paper we include *S. megalura* in the genus *Sylvisorex*.

Comparative material of *S. ollula*. Cameroon: ZFMK 63.190, camp V, above Mueli, northern side of Mount Cameroon, 600 m; ZFMK 63.533, Nyasoso, N Mount Cameroon; ZFMK 99.683, E Nkongsamba, Mount Nlonako, camp near Nguengue, 1200 m, cloud forest; ZFMK 2008.220, Cameroon, Reg. Mamfe, Mukwecha/ Araebisu, 165 m; ZFMK 2008.226, SE Cameroon, Campo Region, Nkoelon, 75 m. Gabon: Equatorial Guinea: CET 736, Monte Alen (LASSO et al. 1996); Nigeria: ZFMK 95.70, SW Obudu Mountains, Boje Forest (06.15 N, 08.55 E), 290 m.

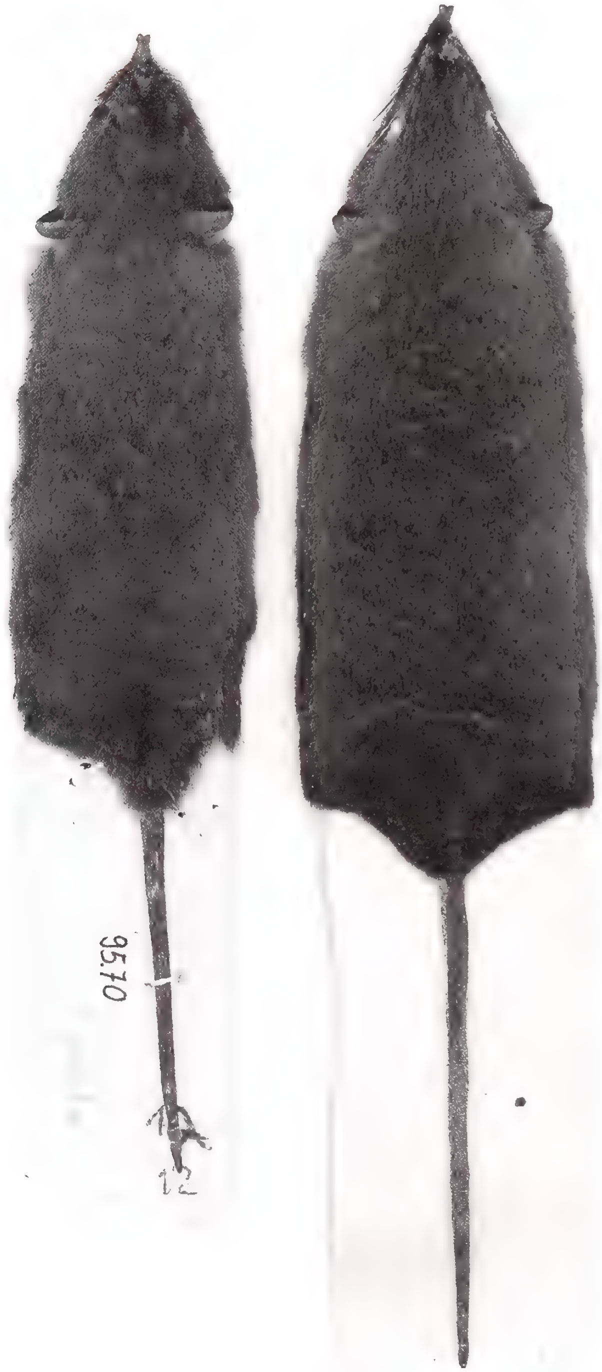

Fig. 1. Flat study skins of a *Sylvisorex ollula* (ZFMK 95.70) from Nigeria and of the holotype of *Sylvisorex corbeti* n. sp. (ZFMK 88.91). Natural size.

3. RESULTS

3.1. A large forest shrew from Nigeria

***Sylvisorex corbeti* n. sp.** (Figs 1, 2, 4, 5)

Holotype and type locality. Skin mounted on cardboard and skull of a young adult female (ZFMK 88.91), collected by G. Nikolaus on 23.03.1988 (field no. GN 60) in forest swamp near Chappa Waddi, (07° 01' N, 11° 41' E), 1 900 m a.s.l., Gotel Mountains, SE Nigeria. The sex of the specimen was previously given as "male" by HUTTERER et al. (1992), but the collector determined it as female.

Measurements of holotype. Body mass 30 g, head and body length 100 mm, tail 64 mm, hindfoot length 17 mm without and 19 mm including claws, ear conch 10 mm.

Diagnosis. A very large and dark blackish brown species of *Sylvisorex* with a total length of 164 mm. Tail of medium length (64 % of head and body length), with no long bristle hairs. Hindfoot long and narrow, metacarpals and metatarsals elongated. Skull large and robust, with a long and wide inter-orbital region, a broad infra-orbital bridge, and a long toothrow. Upper P4 with a large parastyl.

Description. *Sylvisorex corbeti* n. sp. is the largest species of the genus. The head is large, as compared to *S. ollula* (Fig. 1). The colour of the fur is uniformly blackish brown. The hair bases on the dorsum are plumbeous, and the tips blackish brown. No difference in colour exists between dorsum, venter, and limbs. Hairs on dorsum are about 3-4 mm in length. Facial vibrissae reach 27 mm in length. Ear conch has a medium size, is round and pocketed, and covered by very short hairs. Hind foot very long and narrow, with elongated digits and short claws (Fig. 2). Ventral inner surface of hind foot with folds but not covered by small granule-like bumps. Tail of medium length, colour uniform, no long bristle hairs present.

Skull (Fig. 4) very large with a large hexagonal braincase. Dorsal profile (Fig. 5) straight, rostrum long and robust. Interorbital constriction relatively broad (21.2 % of condylo-incisive length, versus 20.7 % in *S. ollula*), its outer margins running almost parallel. Infra-orbital bridge wide, lachrymal foramen large. Maxillary wide compared to *S. ollula*; zygomatic process of maxillary pointed. Superior and inferior articular facets large and robust. Anterior palate with three incisive foramina; one pair between the upper unicuspids, and a single one behind.

Upper teeth: First upper incisor very large, with a long anterior hook and a less prominent talon (Fig. 5). First upper unicuspid very large, second, third and fourth unicuspids much smaller, the third being a little larger than the

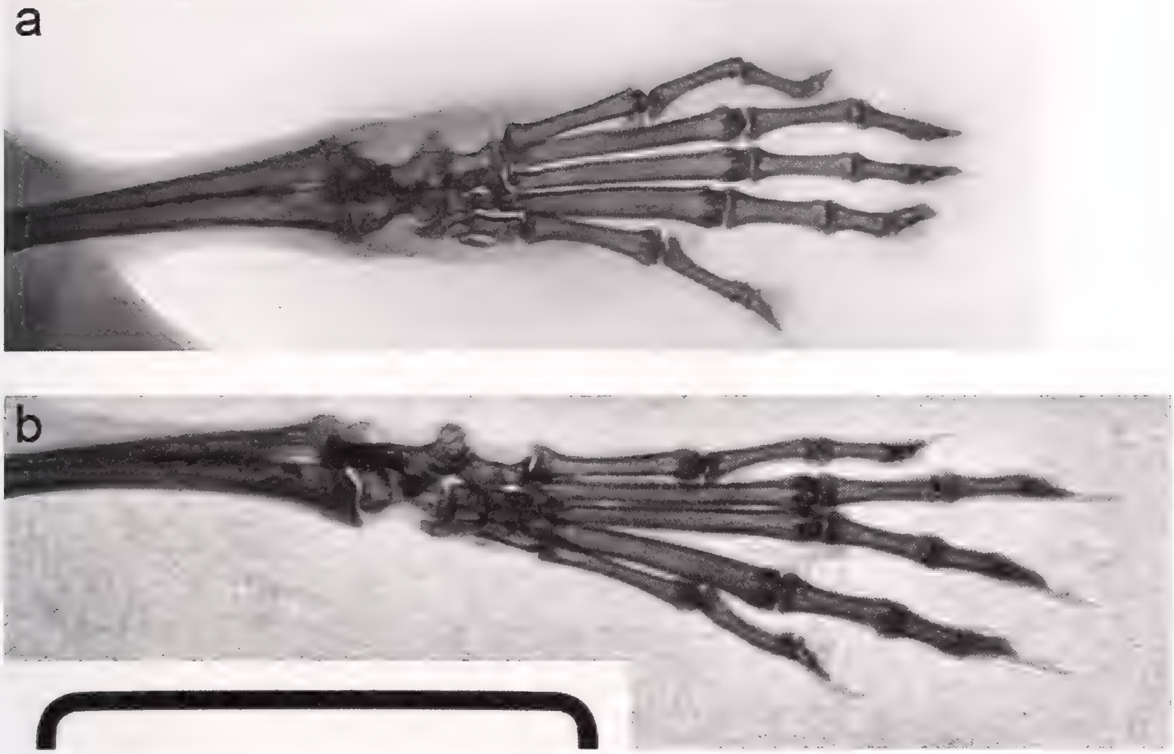

Fig. 2. X-rays of a hindfoot of *Sylvisorex ollula* (ZFMK 2008.226, top) and of *Sylvisorex corbeti* n. sp., (holotype ZFMK 88.91, bottom); scale is 12.8 mm. Note the difference in length of the metacarpals.

Table 1. External measurements (mm) and weight (g) of *Sylvisorex corbeti* n. sp. and of some *S. ollula* from Nigeria and Cameroon.

Species	Origin	TL	HB	Tail	HF	E	WT	Tail/HB
S. corbeti n. sp., ZFMK 88.91	Nigeria	164	100	64	17/19	10	30	64 %
S. ollula, ZFMK 95.70	Nigeria	142	90	52	14/15	8	17	58 %
S. ollula, ZFMK 63.190	NW Cameroon	142	92	50	14/16	8	19	54 %
S. ollula, ZFMK 69.533	NW Cameroon	141	84	57	15/17	8	20	68 %
S. ollula, ZFMK 99.683	NW Cameroon	131	84	47	14/16	8	21	56 %
S. ollula, ZFMK 2008.220	NW Cameroon	141	88	53	14/15	8	16	60 %
S. ollula, ZFMK 2008.226	SE Cameroon	139	83	56	16/17	8	16	67 %

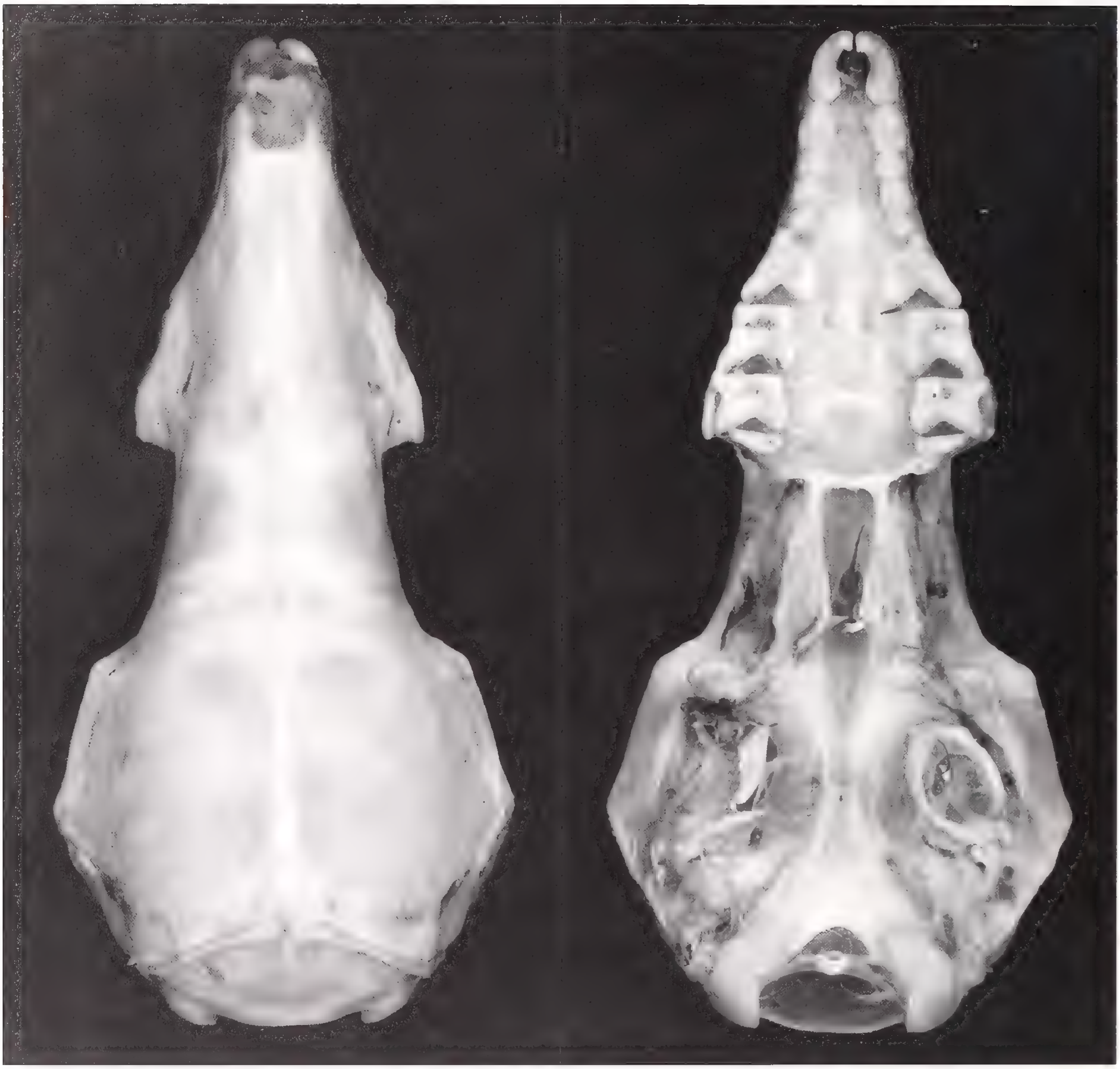

Fig. 3. Skull of *Sylvisorex ollula* (CET 736) from Equatorial Guinea in dorsal and ventral view. Total length of skull 24.62 mm.

second and fourth. P4 large, with a prominent parastyle and a large paracone (or metacone, according to MEESTER 1963). The talon of P4 is longer than in *S. ollula*, extending closer to M1 than in *S.ollula*. M1-2 are large and square-shaped in occlusal view, M3 is short (0. 69 x 1.56 mm in the holotype), but not as reduced as in *S. ollula* (Fig. 4).

Mandible: Robust with a long ramus, a low coronoid process, and a wide angular process. COR 54.7 % of LTR (59.6 % in *S. ollula*). Foramen mentale below posterior root of lower p4. Condyle robust and rectangular, about as wide as high.

Lower teeth: Tip of first incisor curved upwards, with two denticulations on cutting blade. Lower p4 as long as wide (occlusal view). Lower molars long and slender in occlusal view; third lower molar without talonid basin.

Comparisons. *S. corbeti* n. sp. is larger than any other species in the genus, as understood here. It can only be compared with *S. ollula*, which it resembles externally. In absolute external measurements, *S. corbeti* n. sp. is larger and has a longer tail than specimens of *S. ollula* from Nigeria or Cameroon (Table 1), although the relative tail length is similar. Specimens from Gabon and Equatorial Guinea (GOODMAN & HUTTERER 2004, LASSO et al. 1996)

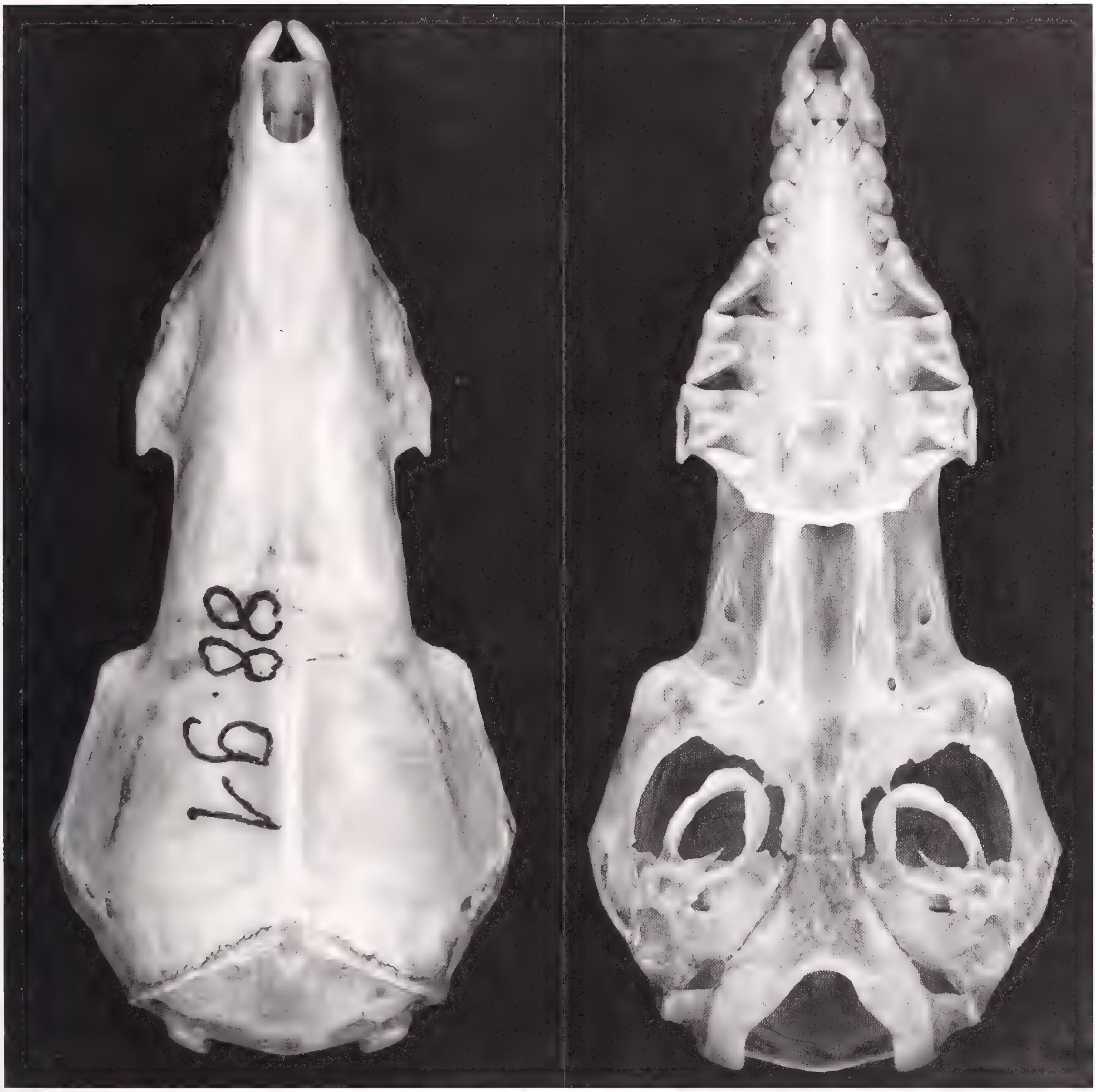

Fig. 4. Skull of *Sylvisorex corbeti* n.sp. (holotype ZFMK 88.91) from SE Nigeria. Total length of skull 26.48 mm.

are smaller also. The fore- and hindfeet of the new species are also considerably longer, due to a prolongation of skeletal elements such as metacarpals and metatarsals (Fig. 6).

The skull of the holotype of *S. ollula* (Thomas 1913) was figured by Jenkins (1984), and another specimen from Equatorial Guinea is shown in Fig. 3. *S. corbeti* n. sp. (Figs 4, 5) is distinguished by size (Table 2), but also by a number of cranial and dental details mentioned above. The largest fossil species, *S. olduvaiensis* Butler & Greenwood, 1979, is considerably smaller (Butler & Greenwood 1979); it has a mean coronoid height of 4.5 mm (5.94 mm in the new species).

Habitat. The holotype was collected in a forest swamp at 1900 m. It shares this habitat with rodents such as *Otomys occidentalis* Dieterlen & Van der Straeten, 1992 and *Praomys obscurus* Hutterer & Dieterlen, 1992.

Etymology. We dedicate this species to Gordon B. Corbet, former curator of mammals at The Natural History

Museum, London. He has served the scientific community for decades by hosting visitors from all around the world at the British Museum mammal collections. Besides writing textbooks on mammals of the Palaearctic and Indomalayan Regions and the World, he has demonstrated his interest in African mammals by careful revisions of hedgehogs, hyraxes, and elephant shrews. He also described the now probably extinct Nigerian pygmy hippopotamus (Corbet 1969).

3.2. A new record of *Sylvisorex ollula* from Nigeria

The presumed record of *S. ollula* from Nigeria (Hutterer et al. 1992) is no longer valid, after our study revealed that the voucher specimen represents a different species described here as new. However, *Sylvisorex ollula* does occur in Nigeria, as a new yet unrecorded specimen demonstrates. During a survey of small mammals of the Boje Forest at 290 m in the SW Obudu Mountains (06.15 N, 08.55 E), G. Nikolaus collected a male of *S. ollula* on 13 January 1995. The specimen (ZFMK 95.70, Fig. 5) is much smaller than *S. corbeti* n. sp. and agrees well with typical *S. ollula* in size (Table 1) and shape of skull (Fig. 5).

4. DISCUSSION

The discovery of *Sylvisorex corbeti* n. sp. further enriches the morphological diversity of the genus, as previously summarized by Hutterer (1985) and Hutterer & Schlitter (1996). With a body mass of 30 g it marks the upper limit of the genus. The new species shows a unique combination of characters of a terrestrial forest shrew (large body, tail of medium length, ear conch of moderate size) with those of scansorial shrews (elongated limbs). The digits of the hindfoot (expressed by the length of metatarsal III) are even longer than in *Sylvisorex megalura* (Fig. 6), a species known for its adaptation for climbing (Vogel 1974). We know nothing about the lifestyle of the new species, except that it lives in forest swamp at 1900 m. It is part of a guild of small mammal species confined to the forested parts of the Mambilla Plateau shared by Nigeria and Cameroon (Hutterer et al. 1992).

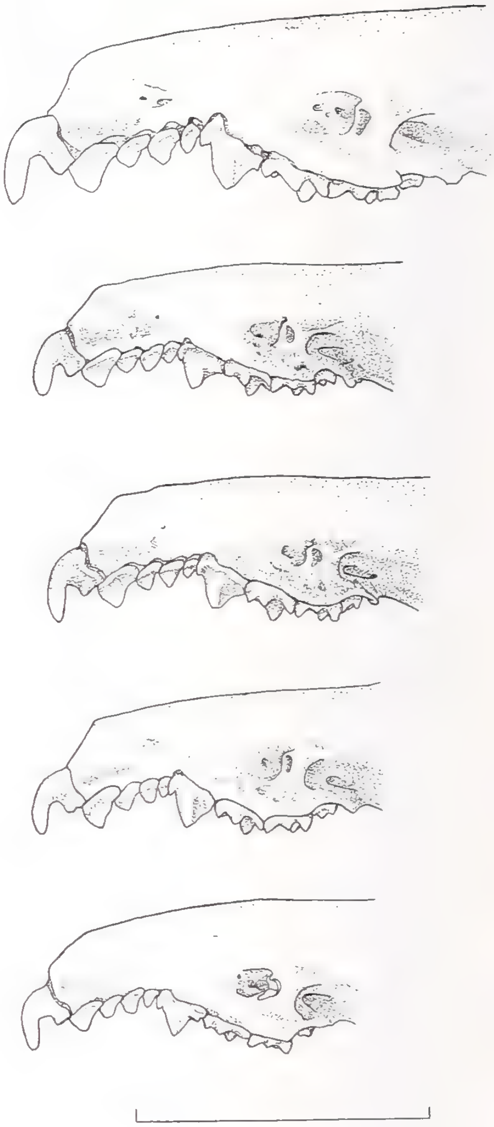

Fig. 5. Lateral views of the maxillary portion of the skulls of (top to bottom) *Sylvisorex corbeti* n. sp. (holotype) and *S. ollula* (ZFMK 95.70, SE Nigeria), ZFMK 69.533 (NW Cameroon), ZFMK 2008.220 (NW Cameroon), and CET 736 (Equatorial Guinea). Scale 10 mm.

The true content of the genus *Sylvisorex* is still not known. New species with surprising adaptations have been discovered in Central Africa (Mukinzi et al. 2009; Hutterer et al. 2009) and add to the diversity of the genus. We included two further undescribed species from D. R. Congo in Fig. 6, to be described in the future. If these and others are included, the number of species of *Sylvisorex* is close to 20. Genetic studies suggest that *S. megalura* may be related to *Suncus* (Querouil et al. 2001), and other authors (Dubey at al. 2008) propose the inclusion of all African *Suncus* and *Sylvisorex* species into one genus. A paraphyly of *Sylvisorex* was already considered by Heim de Balsac & Lamotte (1957). Further problems are posed by the morphologically unique genera *Ruwenzorisorex* Hutterer, 1986 and *Scutisorex* Thomas, 1913, both of which are genetically close to *Sylvisorex*. No conclusive phylogeny is available at this moment, but the study of African forest shrews remains an exciting enterprise.

Table 2. Cranio-dental measurements of *Sylvisorex corbeti* n. sp. and *S. ollula* from Nigeria and Cameroon.

Species	**CI**	**PL**	**UTR**	**P4-M3**	**IO**	**MB**	**GW**	**PGL**	**HCC**	**LTR**	**COR**
S. corbeti n. sp. ZFMK 88.91	26.48	11.59	11.47	6.18	5.61	7.63	11.94	8.13	6.18	10.86	5.94
S. ollula, SE Nigeria ZFMK 95.70	24.26	10.37	10.47	5.61	4.86	7.26	11.02	7.40	5.98	9.84	5.96
S. ollula, NW Cameroon ZFMK 63.190	24.79	10.43	10.76	5.88	5.34	7.60	11.14	7.67	6.19	10.19	6.28
S. ollula, NW Cameroon ZFMK 69.533	24.75	10.61	10.89	5.80	4.98	7.44	–	7.54	5.99	10.32	5.96
S. ollula, NW Cameroon ZFMK 99.683	25.28	11.28	11.01	5.80	4.97	7.17	11.18	7.72	6.21	10.35	5.92
S. ollula, NW Cameroon ZFMK 2008.220	24.10	10.20	10.83	5.97	5.17	7.46	11.36	7.61	5.85	10.76	6.42
S. ollula, SE Cameroon ZFMK 2008.226	24.48	9.73	10.87	5.87	5.16	7.30	11.15	7.46	6.17	10.45	5.97
S. ollula, Equ. Guinea CET 736	24.62	10.40	10.39	5.69	5.14	7.28	11.49	7.66	6.33	9.86	6.21

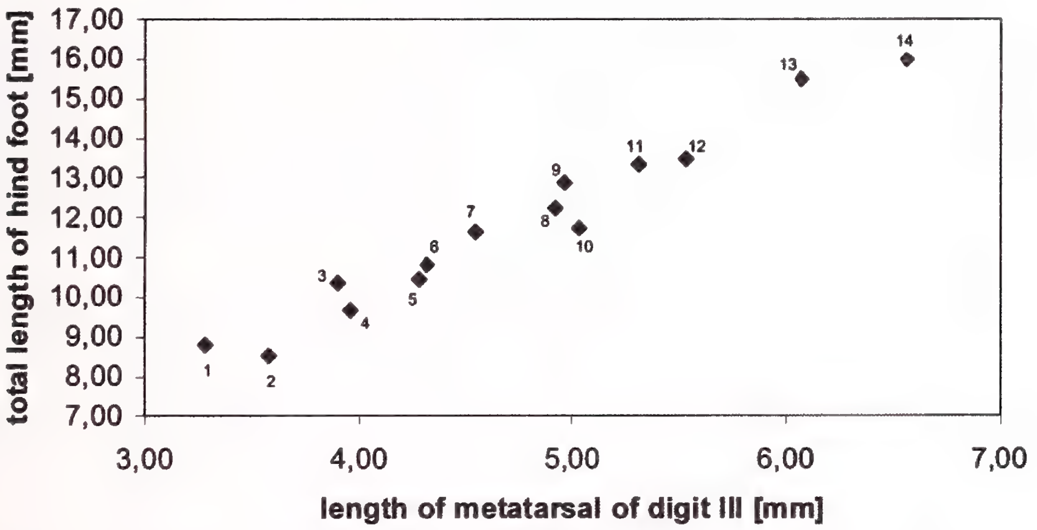

Fig. 6. Relation between length of the metatarsal of digit III and total length of hind foot, as taken from digital X-ray images. 1 *S. akaibei* Mukinzi, Hutterer & Barriere, 2009, 2 *S. johnstoni* (Dobson, 1888), 3 *S. konganensis* Ray & Hutterer, 1996, 4 *S. vulcanorum* Hutterer & Verheyen, 1985, 5 *S. granti* Thomas, 1907, 6 *S.* n. sp. A, 7 *S. morio* (Gray, 1862), 8 *S. camerunensis* Heim de Balsac, 1968, 9 *S. lunaris* Thomas, 1906, 10 *S. isabellae* Heim de Balsac, 1968, 11 *S. ollula,* 12 *S.* n. sp. B, 13 *S. megalura,* 14 *S. corbeti* n. sp.

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Zusammenfassung. Aus dem südöstlichen Hochland von Nigeria wird eine neue Spitzmausart als *Sylvisorex corbeti* n. sp. beschrieben. Das der Beschreibung zu Grunde liegende Tier war zuvor als *Sylvisorex ollula* bestimmt worden, ist aber deutlich größer, besitzt einen längeren Schwanz, verlängerte Hinterfüße und einen sehr großen Schädel und repräsentiert damit die größte Art der Gattung. Ein neues Exemplar aus den Obudu Mountains im südöstlichen Nigeria stimmt morphologisch gut mit typischen *S. ollula* aus den Tieflandregenwäldern des südlichen

Kamerun überein and repräsentiert daher den ersten korrekten Nachweis dieser Art für Nigeria.

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Grimmberger, Eckhard & Rudloff, Klaus, unter Mitarbeit von Kern, Christian (2009). Atlas der Säugetiere Europas, Nordafrikas und Vorderasiens. Natur und Tier Verlag, Münster. 496 S., 437 Karten, 1094 Abbildungen. ISBN 978-3-86659-090-8. Preis 98,00 €.

Auf dieses Werk haben Insider schon lange gewartet. Der Ehrgeiz, alle Säugetierarten Europas, Nordafrikas und Vorderasiens in farbigen Lebendfotos zu dokumentieren, führte die beiden Verfasser schon seit vielen Jahren in zahlreiche Länder Europas, Nordafrikas und Asiens. Eckhard Grimmberger hat seine fotografische Meisterschaft bereits früher mit einem Buch über die Fledermäuse Europas (Schober & Grimmberger 1998), das in vier Sprachen übersetzt wurde, unter Beweis gestellt. Klaus Rudloff hat als Kurator im Tierpark Berlin Zugang zu vielen seltenen Säugetieren gehabt und diese im Foto dokumentiert. Was nicht durch eigene Tätigkeit im Foto zu bekommen war, ergänzten viele Zoologen aus der ganzen Welt.

Das vorliegende Buch erweitert den geografischen Rahmen über Europa hinaus und schließt die nordafrikanischen Länder von Marokko bis Ägypten und die vorderasiatischen Länder von Jordanien bis Aserbaidschan ein. Möglich wurde dies auch durch das taxonomische Referenzwerk „Mammal Species of the World“ (Wilson & Reeder 2005), das einen leichten Zugang zur Nomenklatur und Verbreitung aller Säugetierarten erlaubt. Im Fahrtwind dieses Werkes sprossen seit 2005 etliche Säugetierführer aus dem Boden, von denen der vorliegende einer der originellsten ist.

Das Buch beginnt mit einleitenden Kapiteln (Einführung, Prinzipien der zoologischen Systematik, Die Welt der Säugetiere, Säugetierschutz, Zur Benutzung des Buches), die für Laien verständlich sind, aber auch Studenten der Zoologie noch genügend Stoff vermitteln könnten. Den Hauptteil des Buches bilden mit über 400 Seiten Artkapitel von mehr als 400 Säugetierarten, die der Systematik der bereits genannten Weltliste von Wilson & Reeder folgen. Jedes Artkapitel enthält neben dem wissenschaftlichen Namen einen Trivialnamen in deutscher, englischer, französischer, russischer und spanischer Sprache, eine kurze Beschreibung des Tieres, sodann Angaben zu Verbreitung, Lebensraum und Lebensweise, Schutzstatus und weiterführender Literatur, begleitet von einer farbigen Verbreitungskarte und einem oder mehreren Farbfotos. Diese Fotos sind durchweg von hoher Qualität und bilden einen Schatz, wie er bisher in dieser Art nicht verfügbar war. Viele seltene Säugetierarten sieht der Leser hier zum ersten Mal, so z. B. *Meriones grandis, Gerbillis hoogstraali, Mesocricetus raddei, Microtus anatolicus* und andere. Die Vielfalt der Nagetiere wird erst durch Lebendaufnahmen richtig erfahrbar. Die Schönheit und Vielfalt der Pferdespringer, Springmäuse, Rennmäuse, Hamster oder Blindmäuse ist überwältigend. Das gilt aber auch für die anderen Gruppen, seien es Igel, Spitzmäuse, Maulwürfe, Fledermäuse, Hasenartige, Huftiere, oder Karnivoren, je nach Vorliebe. Im Buch nicht berücksichtigt sind die Walartigen.

Originell sind auch die Anhänge, die die Feldbestimmung erleichtern sollen. Sie zeigen Schwänze von Springnagern und Rennmäusen, Hinterfuß-Sohlenschwielen von Nagetieren, Zahn- und Schädelmerkmale von einigen Kleinsäugern, sowie die Spiegel von Hirschen. Alle Anhänge zeigen Detailansichten in Farbfotos. Ein Literaturverzeichnis und ein Register beschließen diesen wunderbaren Atlas, der uneingeschränkt empfohlen werden kann. Das Buch ist für ein breites Leserpublikum von Interesse, und auch der Spezialist wird Bilder und Informationen finden, die für ihn neu sind. Eine Ausgabe in englischer Sprache würde den Leserkreis noch um ein vielfaches erweitern.

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Temple, Helen J. & Cuttelod, Annabelle (compilors) (2009). The Status and Distribution of Mediterranean Mammals. Gland, Switzerland and Cambridge, UK, IUCN. vii + 32 pp. ISBN 978-2-8317-1163-8. Available from IUCN, Publications Services, 28 Rue Mauverney, 1196 Gland, Switzerland.

This booklet presents the results of a Mediterranean Mammal Red List workshop held in Malaga, Spain, in 2007. This workshop was embedded in the Mediterranean Biodiversity Assessment and in Global Mammal Assessment activities of the IUCN, in cooperation with experts from around the world. The aim of this workshop was to assess the taxonomy, distribution, and conservation status of all mammal species living in the 31 countries bordering the Mediterranean Basin from Albania to Turkey, and including the Atlantic Islands and Western Sahara. A total of 297 species was assessed, excluding species of marginal occurrence in the region.

16.5% of the Mediterranean mammals are threatened with extinction at the regional scale, and a further 8% are Near Threatened. By comparison, 56% of dolphins and whales, and 5% of birds are threatened with extinction. More than one-quarter (27%) of the Mediterranean mammals have declining population, and 31% are stable. The mammals of the Magreb region were included in the assessment, and this region holds a large number of endemic species, unique to the Mediterranean and found nowhere else. In the Sahara, species richness is relatively low, but a high proportion of Saharan species are threatened.

The booklet includes many more interesting data and maps showing the geographic distribution of species richness and endemic species richness in the Mediterranean Region. An appendix lists all mammal species considered and their Red List status. Copies of this useful summary can be obtained from IUCN.

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Bonn

On Agamid Lizards

Proceedings of 'DeAgamis –
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held in the Zoologisches Forschungsmuseum
Alexander Koenig in Bonn,
February 22–24, 2008

De Agamis

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Philipp Wagner,
Thomas M. Wilms &
Wolfgang Böhme

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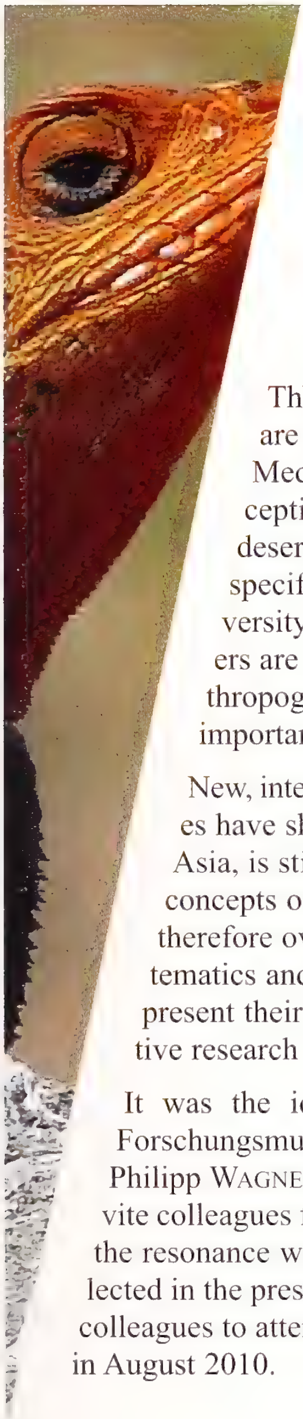


PREFACE

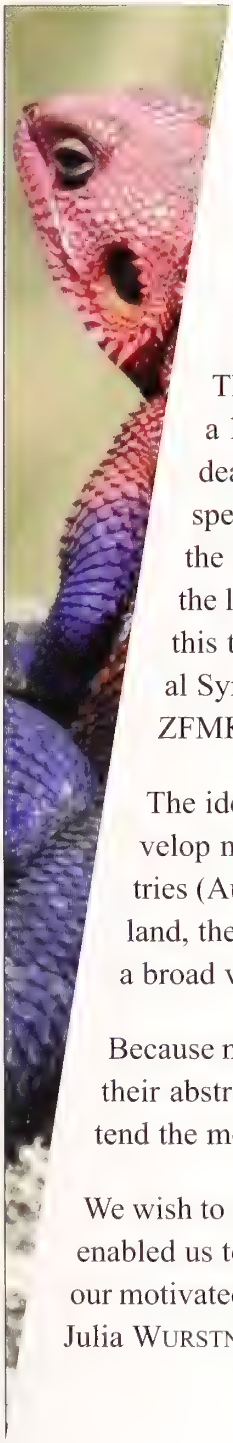
The iguanian lizard family Agamidae exists in more than 350 species which are grouped in about 45 genera. Agamid lizards are distributed through the Mediterranean, subtropical and tropical regions of the Old World with the exception of Madagascar. They occupy a great variety of biotopes ranging from deserts through steppes and savannas to tropical rain forest. The adaptations to specific habitats have led to an extraordinary morphological and ecological diversity. Agamids may be wide-ranging or confined to biodiversity hotspots, others are relictual endemics to small areas. Many of them, however, are under anthropogenic pressure, either by habitat loss or by direct persecution, thus being important for the conservation of biodiversity on a global scale.

New, intensive studies with multiple methods including molecular genetic approaches have shown that the taxonomic diversity of agamids, in Africa as well as in SE Asia, is still considerably underestimated. Also some phylogenetic hypotheses and concepts of the last decades have been challenged by new, current research. It was therefore overdue that the herpetologists working on various aspects of agamid systematics and biology in various parts of the world were brought together in order to present their results and ideas to each other and to create a new network of cooperative research on agamids (in Latin "de agamis").

It was the idea and initiative of the Herpetology Section of the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), in particular of the young researcher Philipp Wagner who devoted a part of his PhD thesis to these fascinating lizards, to invite colleagues from many countries to a first international symposium "DeAgamis", and the resonance was very good. A part of the scientific outcome of this symposium is collected in the present issue of Bonner zoologische Beiträge. I hope this issue will stimulate colleagues to attend a second symposium DeAgamis which I am inviting to St. Petersburg in August 2010.

St. Petersburg, October 2009

Prof. Dr. Natalia B. Ananjeva



EDITORIAL

The Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) has established a long tradition in organizing and hosting international symposia. Most of these dealt with tropical zoology and often focussed on Africa and on vertebrates. Some special symposia were devoted to herpetology, the first of these to the reptiles of the Canary Islands, three further ones to all aspects of monitor lizard research, and the last one to the world's widest-distributed lizard, the lacertid *Zootoca vivipara*. In this tradition, one of us (Philipp WAGNER) developed the idea of a First International Symposium on Agamid Lizards (his favourite squamate group) which was held at ZFMK on February 22–24, 2008 under the name "DeAgamis".

The idea to bring the world's leading specialists on agamid lizards to Bonn and to develop new cooperation projects had a very positive echo. 50 researchers from 9 countries (Australia, Czech Republic, England, Germany, The Netherlands, Russia, Switzerland, the USA and Vietnam) attended, and a total of 20 talks and posters which covered a broad variety of topics on nearly all agamid groups were presented to the participants.

Because not all contributors were able to submit their presentations to the present volume, their abstracts are summarized in an appendix in order to inform the readers who did attend the meeting, and about the topics presented and discussed.

We wish to thank the Deutsche Forschungsgemeinschaft (DFG) for providing the funds that enabled us to invite speakers from abroad and even overseas. Moreover, we are indebted to our motivated and effective student crew, especially to Michael BAREJ, Monique HÖLTING and Julia WURSTNER.

Partcipants of DeAgamis in Bonn, February 23rd, 2008.

Finally, we are happy to inform the readers that there will be a second International Symposium on Agamid Lizards (DeAgamis II) to be organized by our friend and colleague Prof. Dr. Natalya B. Ananjeva in St. Petersburg in 2010 which lets us hope that our first symposium DeAgamis might evolve into a series of meetings.

Ph. Wagner

Bonn, October 2009 Philipp Wagner, Thomas Wilms & Wolfgang Böhme

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Studies on African *Agama* V.
On the origin of *Lacerta agama* Linnaeus, 1758 (Squamata: Agamidae)

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Abstract. Herein we present our strategy to preserve the nomenclatural stability of the widespread and common Afrotropical lizard *Agama agama* (Linnaeus, 1758). We recognized several proposed syntypes, belonging to a variety of species, i.e., *Agama agama*, *Agama atra* and *Tropidurus plica*. But we have shown that these specimens do not belong to the type material. However, if they were included in the type material the selection of the e.g. American syntype, *Tropidurus plica* – a tropidurine iguanid, as lectotype would result in taxonomic chaos, as *Agama agama* is an African species and includes in its synonymy the type species of the type genus of the family Agamidae. The illustrated types in Seba (1734) are recognized by us as a variety of agamid lizards with a type locality encompassing the New and the Old World and not simply 'America', as given by Linnaeus.
Morphologically, *Agama agama* is highly variable making it impossible to assign the syntype that agrees with the current concept of *Agama agama* to a geographic population, particularly as the only character, viz. the colour pattern, is no longer discernible in this specimen. This endangers the stability of the known subspecies of *Agama agama*. We therefore designate a neotype for *Lacerta agama* Linnaeus, 1758 herein.

Keywords. Nomenclature; taxonomy; neotype; Squamata; Agamidae; *Agama agama*; African rainbow lizard; type locality; Africa.

INTRODUCTION

The genus *Agama* Daudin, 1802 is one of the most widely distributed lizard genera within Africa, although the relationships between the species in the genus are still poorly known. *Agama* is a highly taxonomically complex genus and most of the taxa are very similar and highly variable in pholidosis and only identifiable by the nuptial colouration of males (McLachlan 1981, Jacobsen 1992, Wagner 2007). Therefore, it is often not possible to assign a single specimen with colouration lacking to a particular species or subspecies. This situation causes problems in the determination of type material to assess the validity of the different taxa. Thus, in many species and subspecies validity is doubtful (e.g., *Agama bocourti* Rochebrune, 1884; *Agama cornii* Scortecci, 1928; *A. picticauda* Peters, 1877; *A. congica* Peters, 1877). Past generic reviews have only been attempted for some species groups (Boulenger & Power 1921, Grandison 1956, 1968) and most workers have considered it pointless to designate lecto- or neotypes to stabilize the nomenclature of the taxa. As an example, Grandison (1968) designated a lectotype of *Agama benueensis* Monard, 1951 (today recognized as a subspecies of *Agama doriae* Boulenger, 1885; see Moody & Böhme 1984), thereby stabilizing another *Agama* species because several individuals of the type series were identified as *A. paragama* Grandison, 1968. However, the situation has changed and several authors are now working on a broad scale phylogeny of the entire genus (Wagner & Leaché, own data). For this analysis it is essential to clarify the taxonomic status of *Agama agama* (Linnaeus, 1758) because many taxa are assigned to this species as synonyms or subspecies. Even in recent years several former subspecies of *A. agama* have

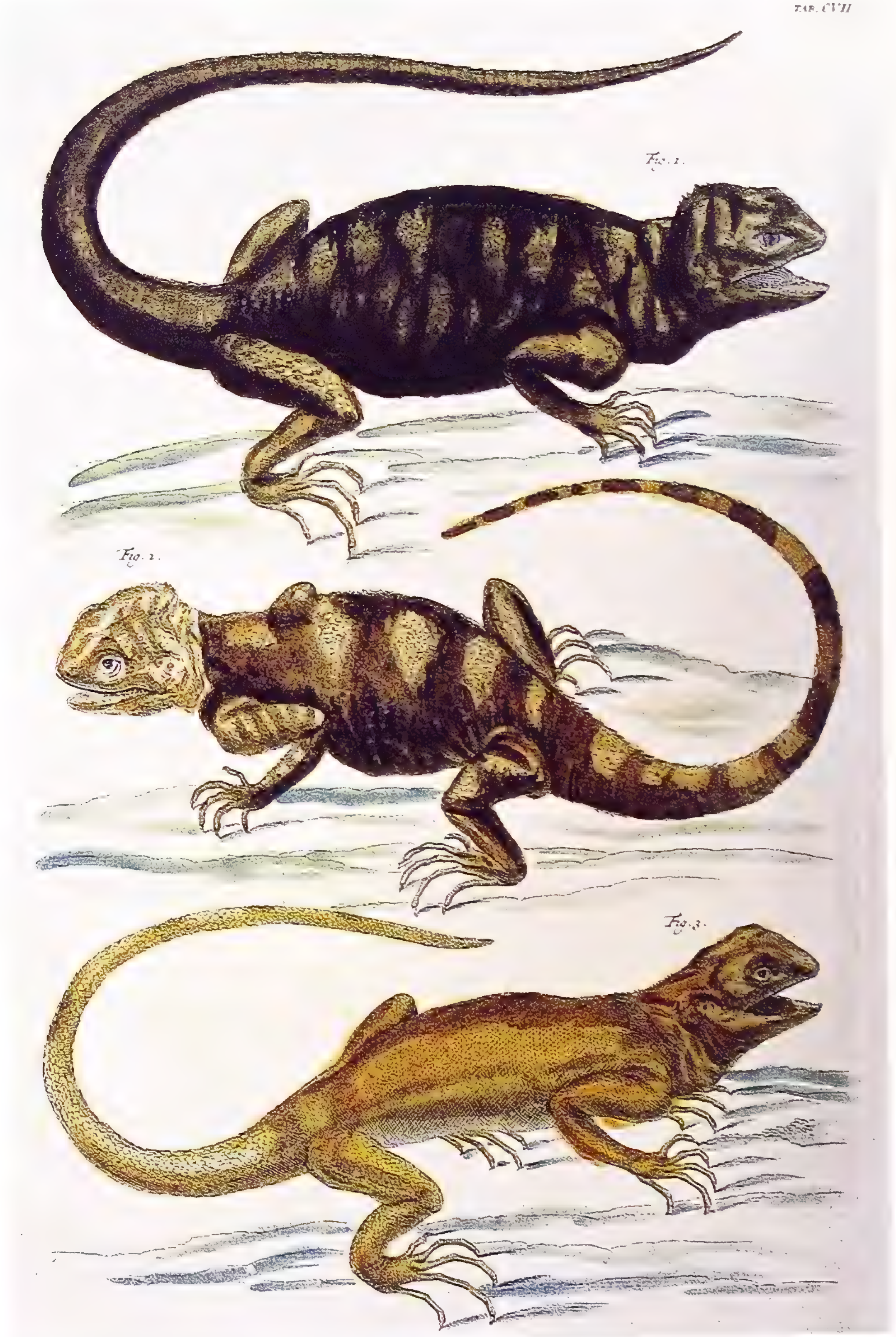
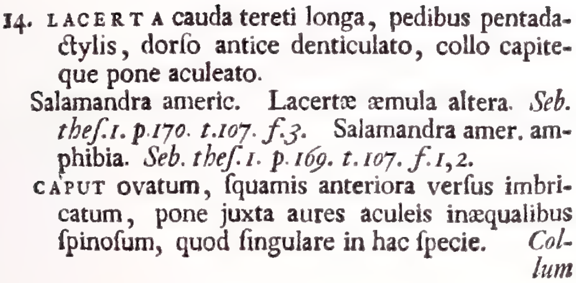

TAB. CVII
Fig. 1.
Fig. 2.
Fig. 3.

Fig. 1. Plate 107 published in *Thesaurus* I by Seba (1734) showing three lizards described as '*Salamandra Americana, posteriore parte Lacertum referens, amphibia; mas*'.



14. LACERTA cauda tereti longa, pedibus pentadactylis, dorſo antice denticulato, collo capiteque pone aculeato.
Salamandra americ. Lacertæ æmula altera. *Seb. theſ.1. p.170. t.107. f.3.* Salamandra amer. amphibia. *Seb. theſ.1. p.169. t.107. f.1,2.*
CAPUT ovatum, ſquamis anteriora verſus imbricatum, pone juxta aures aculeis inæqualibus ſpinoſum, quod ſingulare in hac ſpecie. *Collum*

Fig. 2. Description of '*Lacerta amphibia*' in the '*Amoenitates academicæ*' by LINNAEUS (1749, Vol. 1, p. 288).

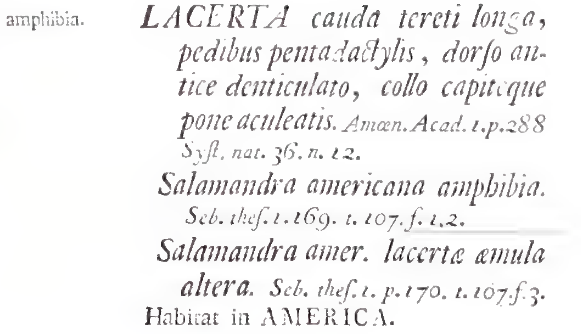
been recognized as species. BÖHME et al. (2005) have elevated the *Agama lionotus* Boulenger, 1896 complex (*Agama lionotus lionotus* Boulenger, 1896, *Agama l. elgonis* Lönnberg, 1922, *Agama l. dodomae* Loveridge, 1923, *Agama l. ufipae* Loveridge, 1932) leaving the true *Agama agama* to full species rank, with the following several nominal subspecies of its own: *Agama agama agama* Linnaeus, 1758; *Agama a. africana* Hallowell, 1844 (type locality: Liberia); *Agama a. boensis* Monard, 1940 (type locality: Madina Boé, Guinea-Bissau) and *Agama a. mucosoensis* Hellmich, 1957 (type locality: Mucoso near Dondo, Angola). *Agama a. savattieri* Rochebrune, 1884 [type localities: Casamance (Senegal?), Mélacorée (Guinea?), Albréda (The Gambia), Bathurst (=Banjul, The Gambia] has been synonymized with *A. agama africana* by GRANDISON (1968).

Even the status of these subspecies remains unclear and is dependent on the definition of *A. agama*. Therefore, it is essential to consult the original description by LINNAEUS (1758), the type specimens and previous descriptions of the species. The results of this search are herein presented.

1. PRE-LINNAEEN (BEFORE 1758) NAMES

'*Salamandra americana* Seba, 1734'

In his *Thesaurus* SEBA (1734) published a plate (thes. I, p. 170, t. 107) depicting three lizards (see fig. 1) which he described as '*Salamandra Americana, posteriore parte Lacertum referens, amphibia; mas*'. The *Thesaurus* is published in two separate editions, one in French and Latin, the other one in Dutch and Latin. We herein recognize the Dutch edition because this would be the text that probably most accurately reflects SEBA's own language. In the Dutch part of the accompanying text he described the species shown in figure one of the plate as the '*West-Indische Salamander*' (= West Indian salamander), half salamander, half lizard. The specimens shown in figures two and three of the same plate (herein fig. 1) were also recognized as *Salamandra americana* but the figure captions were '*Wyfie van den voorgaanden Salamander*' (= the female of the above mentioned salamander) (figure two) and '*Ander soort van West-Indischen Salamander als de voregi*' (= another species as the previous one of the west Indian salamander) (figure three).



amphibia.

LACERTA cauda tereti longa, pedibus pentadactylis, dorſo antice denticulato, collo capiteque pone aculeatis. *Amæn. Acad. 1. p. 288 Syſt. nat. 36. n. 12.*
Salamandra americana amphibia. Seb. theſ. 1. 169. t. 107. f. 1, 2.
Salamandra amer. lacertæ æmula altera. Seb. theſ. 1. p. 170. t. 107. f. 3.
Habitat in AMERICA.

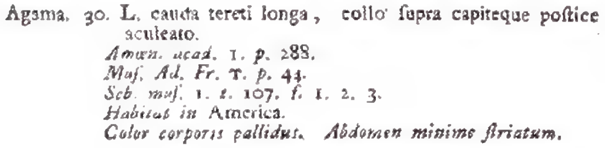
Fig. 3. '*Lacerta amphibia*' published in the 'Museum Adolphi Friderici' (LINNAEUS 1754, p. 44) with the first mention in of the locality 'Habitat in America'.

All the subsequent descriptions of the species refer to this plate and the text mentioned. The name '*Salamander americana*' is mentioned later by many authors (see below).

However, confusions among agamids, geckos and salamanders were common during the 18th and early 19th centuries. As an example, a gecko, today known as *Hemidactylus platyurus*, was described in an agamid genus as *Stellio platyurus* by SCHNEIDER (1792). In the same work SCHNEIDER (1792) also described *Stellio fimbriatus* from Madagascar, today known again as a member of the geckonid genus *Uroplatus*. Also *Trapelus savignyi* AUDOUIN, 1827, described in an agamid genus but in a gecko section of the text is today known as synonym of the gecko *Stenodactylus sthenodactylus* (Lichtenstein, 1823) (WAGNER & CROCHET 2009).

'*Lacerta amphibia* Linnaeus, 1749'

In the '*Amoenitates academicæ*', LINNAEUS' first important contributions as collected theses in seven volumes on systematics, he (LINNAEUS 1749, Vol. 1, p. 288; see fig. 2) described the lizard which was shown in SEBA (1734) as '*Lacerta cauda tereti longa, pedibus pentadactylis, dorso antice denticulato, collo capiteque pone aculeato*' later known as '*Lacerta amphibia*' and synonymised the



Agama. 30. L. cauda tereti longa, collo ſupra capiteque poſtice aculeato.
Amœn. acad. 1. *p.* 288.
Muſ. Ad. Fr. 1. *p.* 44.
Seb. muſ. 1. *t.* 107. *f.* 1. 2. 3.
Habitat in America.
Color corporis pallidus. Abdomen minime ſtriatum.

Fig. 4. Description of *Lacerta agama* in the nomenclaturally binding 10th edition of LINNAEUS 1758 (p. 207).

name '*Salamandra americana*'. In naming his species LINNAEUS referred to the plate published by SEBA (1734, plate 107; see fig. 1 herein) and obviously followed the suggestions of SEBA (1734), considering this species half salamander and half lizard. But LINNAEUS (1749) also referred to the differences between the specimens shown in the figures in SEBA (1734) as he synonymised figure three as *Salamandra americana* and figures one and two as *Salamandra americana amphibia*. Several years later, LINNAEUS (1754, p. 44) published his '*Museum Adolphi Friderici*'. Herein, he added a type locality as 'Habitat in America' and again he referred to two taxa (*Salamandra americana amphibia*, fig. 1 & 2; *Salamandra americana lacerate aemula*, fig. 3).

2. LINNAEUS (1758)

Lacerta agama Linnaeus, 1758

In the 10th and currently still binding edition of his guiding work, LINNAEUS (1758, p. 207) again re-named '*Lacerta amphibia*' to the currently valid *Lacerta agama* Linnaeus, 1758 (see fig. 4). In contrast to the descriptions before, he referred all the three images of plate 107 in SEBA (1734) to this monotypic species and mentioned again '*America*' as type locality. In his description, LINNAEUS (1758) did not refer to other images or vouchers of a museum collection. Therefore, the individuals which are the basis of the illustrations in SEBA (1734) are the syntypes, because the 'International Code of Zoological Nomenclature' (ICZN 1999) does not recognize 'iconotypes' and no other types are mentioned. However, QUENSEL, director of the Swedish Academy of Science from 1799 to 1806, also mentioned three specimens (QUENSEL 1802, QUENSEL in ANDERSSON 1900) from the collection of the Museum Adolphi Friderici in Drottningholm and noted 'that they are identical with Linnaeus's *Lacerta amphibia*' (ANDERSSON 1900, p. 11). However, the use of '*identical*' here only means identical to species not identical type specimens. ANDERSSON (1900) examined these specimens and identified two as 'true *Agama colonorum* Daudin, 1802' and the last as '*Uraniscodon plica* Linnaeus, 1758'. A recent examination by us of the three specimens (Museum Adolphi Friderici: NRM 107, 108, 112; see fig. 5 herein) revealed that they represent three different valid species: *Agama* cf. *agama* (LINNAEUS, 1758), *Agama atra* Daudin, 1802 and *Tropidurus plica* (Linnaeus, 1758). But two of these specimens are without doubt not identical with the individuals illustrated in SEBA (1734). As it is obvious, the lizards shown in figures one and two clearly have segmented tails, which are not only lacking in the three museum vouchers, but also in the genus *Agama* in general. These segmented tails, which are arranged in whorls, are typical for the species of the genera *Acanthocercus* Fitzinger, 1843 and *Laudakia* Gray, 1845 (both Agamidae) occurring in Africa, Asia and Europe. Only the specimen of figure three shows a tail typical for *Agama*, but also for the South American genus *Tropidurus*. These differences were also recognized by DUMÉRIL & BIBRON (1837) who referred the specimens shown in figures one and two of plate 107 in SEBA (1734) to *Stellio vulgaris* Sonnini & Latreille, 1802 (today known as *Laudakia stellio vulgaris*) and erroneously synonymised *Lacerta amphibia* with *Agama colonorum*, as they only referred figure three to *Agama colonorum*.

However, it is obvious by comparing the NRM specimens with the remaining image in SEBA (1734) that it is not identical with one of the specimens. The *atra* specimen has a very different colouration, whereas the *plica* one has the mouth closed, but similar in scalations to the figured specimen. The cf. *agama* specimen is not identical in head scalation and proportion.

Consequently, the NRM specimens are not identical with the lizards shown in SEBA (1734) and are not type specimens of *Lacerta agama* Linnaeus, 1758. As a nomenclatural stabilization of this name is indispensable for further research, a neotype is designated by us (see below).

However, even if e.g. the most similar NRM voucher (the *T. plica*-specimen) to the remaining image were the name-bearing type of *Lacerta agama*, it would require suppression because it would destabilise two well known species, two genera and two families.

Thus *Tropidurus plica* (as currently known) would become *Lacerta agama*. However, *Agama colonorum*, a synonym of *Lacerta agama* today known as *Agama agama*, is also the type species of the genus *Agama*. Therefore, *Tropidurus plica* and closely related taxa like *T. lumaria* and *T. umbra* would become members of the genus *Agama*.

Further, the genus *Agama* is the type genus of the lizard family Agamidae. This would mean that these Old World lizards would lose their name to a New World genus, which would cause a taxonomic chaos and is therefore obviously unacceptable.

According to article 75.6 of the ICZN this approach should not be taken into consideration because it endangers the stability of the well known species *T. plica*, the genus *Agama* and the family Agamidae.

Remarks on the identity of the NRM specimens

As shown above, two of the specimens are not identical with *Agama agama* as they are identified as *A. atra* and *Tropidurus plica*. The remaining voucher (fig. 5c) is a true *Agama* species, and probably *Agama agama* itself. It is obvious from figure 5c that the specimen is in good condition but completely lacking colouration. As previously noted, species of the genus *Agama*, and especially *Agama agama*, are characterized by a high variability of scale counts (BOULENGER & POWER 1921, THYS VAN DEN AUDENAERDE 1963, GRANDISON 1968, MOODY & BÖHME 1984, BÖHME et al. 2005) and therefore nearly all taxa are determined by aspects of colouration of adult males (MCLACHLAN 1981, JACOBSEN 1992, WAGNER 2007). Thus, it is not possible to assign this voucher to a specific *Agama agama* population or subspecies and even not clearly to *Agama agama* itself.

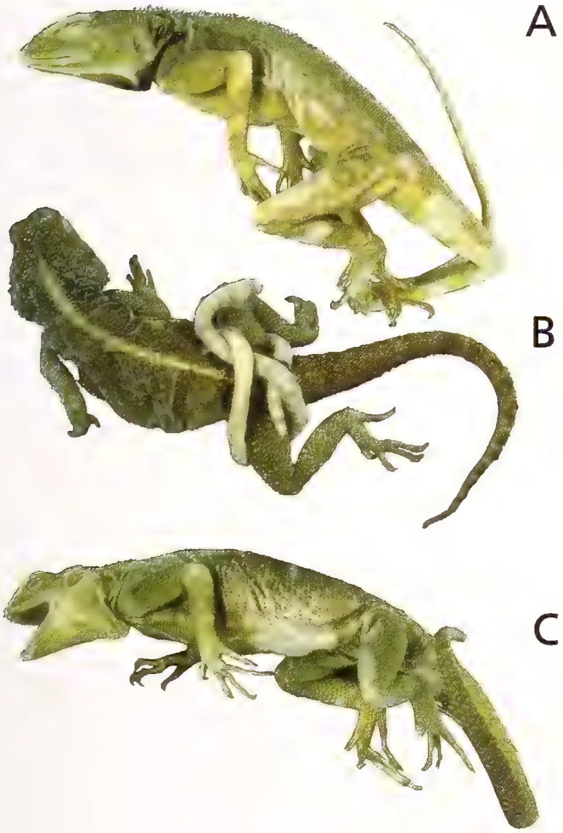


Fig. 5. Formerly supposed syntypes of *Lacerta agama* Linnaeus, 1758 in the Museum Adolphi Friderici (NRM 107, 108, 112). A= *Tropidurus plica* (Linnaeus, 1758); B= *Agama atra* Daudin, 1802; C= *Agama* cf. *agama* (Linnaeus, 1758).

Remarks on the erroneous type locality 'America' & the nomen Agama

Today it is obvious that the type locality 'in America' is erroneous and does not correspond with the actual distribution of the species, genus and family. Surprinsingly, *Agama colonorum* Daudin, 1802, the first available synonym of *Agama agama*, was also described from 'l'Amerique méridionale', 'Cuba' and 'Jamaique'. DAUDIN (1802) suggested this name for *Lacerta agama* Linnaeus, 1758 and mentioned several names (e.g. *Lacerta agama*; *Iguana cordylina* Laurenti, 1768; '*Salamandra americana* Seba, 1734'; *Lacertus major* Sloane; Guana lizard Brown; Blue lizard Edwards; L'agame Daubenton; L'agame ou caméléon de Mexique Stedman) as synonyms. Additionally, DAUDIN (1802) also mentioned aspects of the linguistic usage of the name 'agama' and mentioned that the name is used for a variety of different lizard species in South America. However, the source of the name 'agama' is from the Ewe language of the Kwa group, spoken in Togo, Benin and Ghana (BAUMANN 1936, WESTERMANN 1954). DUMÉRIL & BIBRON (1837) were the first who recognized that the type locality is in error and mentioned a distribution of the species 'sur la côte de Guinée et au Sénégal' (= at the coast of Guinea and in Senegal).

However, the consideration of the type locality as 'in error', the simplest solution, does not solve the problem. According to article 76 of the code, the 'type locality of a nominal species-group taxon is the geographical place of capture, collection or observation of the name-bearing type; if there are syntypes and no lectotype has been designated, the type locality encompasses the localities of all of them'. As the syntypes are not available, the type locality can only be concluded from the identified lizard genera shown on the plate in SEBA (1734).

MERTENS (1938) also recognized the problem and restricted it to 'Cameroon', but without the designation of a lecto- or neotype. According to article 76 of the code, MERTENS' (1938) restriction was invalid and the type locality thus still not clarified.

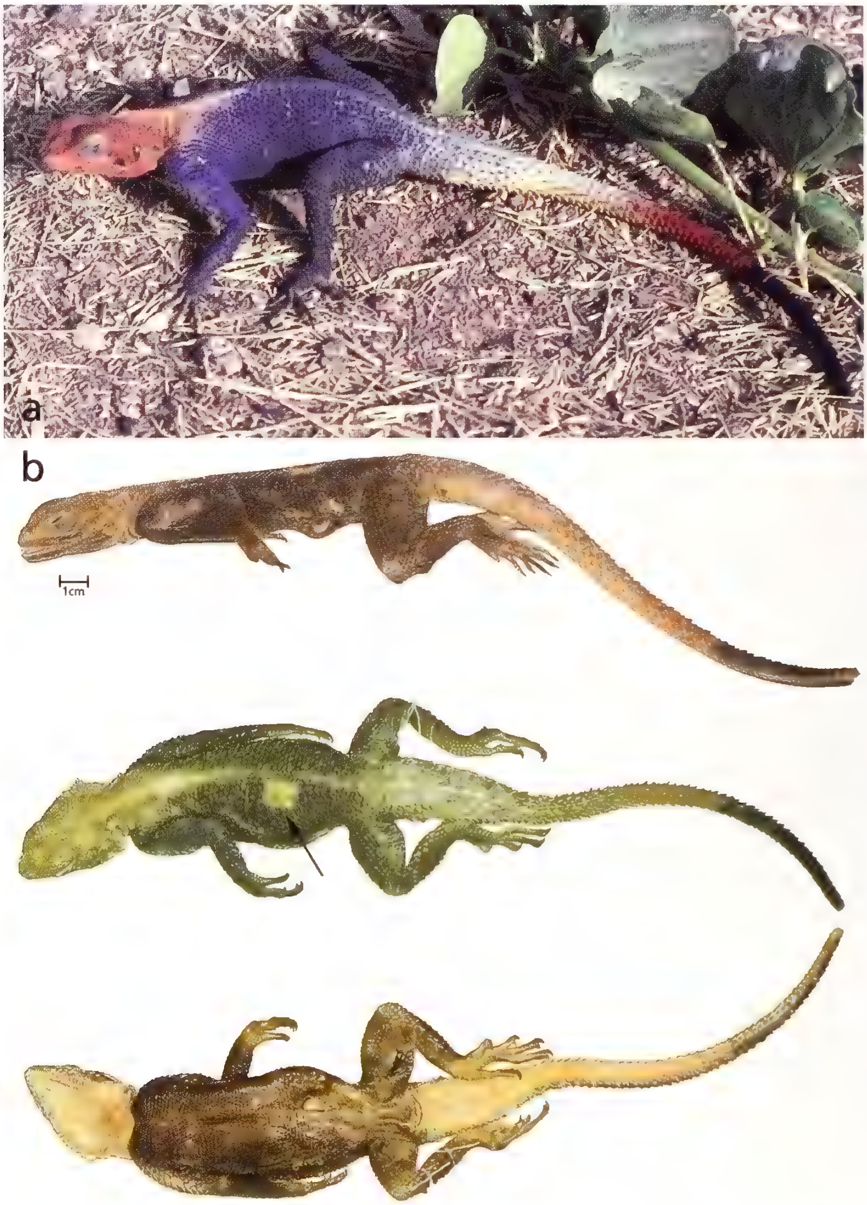


Fig. 6a. Neotype of *Lacerta agama* Linnaeus, 1758 (ZFMK 15222): a = image of the living neotype; b = complete lateral, dorsal (arrow indicates the place of scales used for SEM images, see fig. 6c), ventral body views.

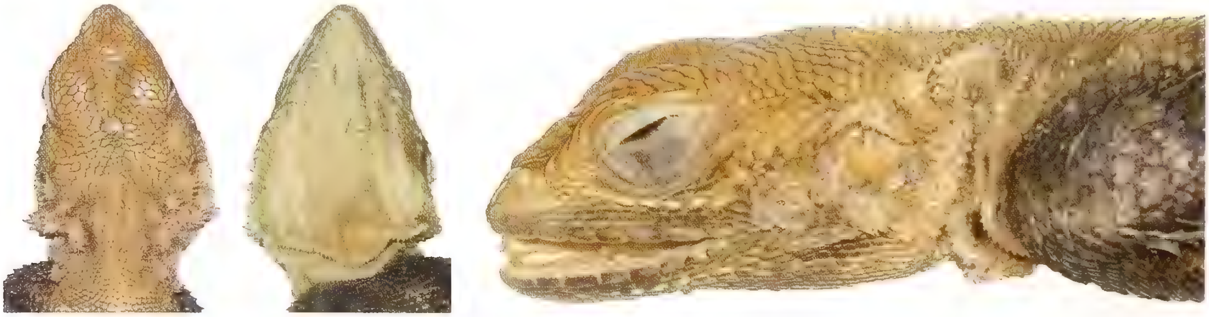


Fig. 6b. Neotype of *Lacerta agama* Linnaeus, 1758 (ZFMK 15222): details of head scalation.

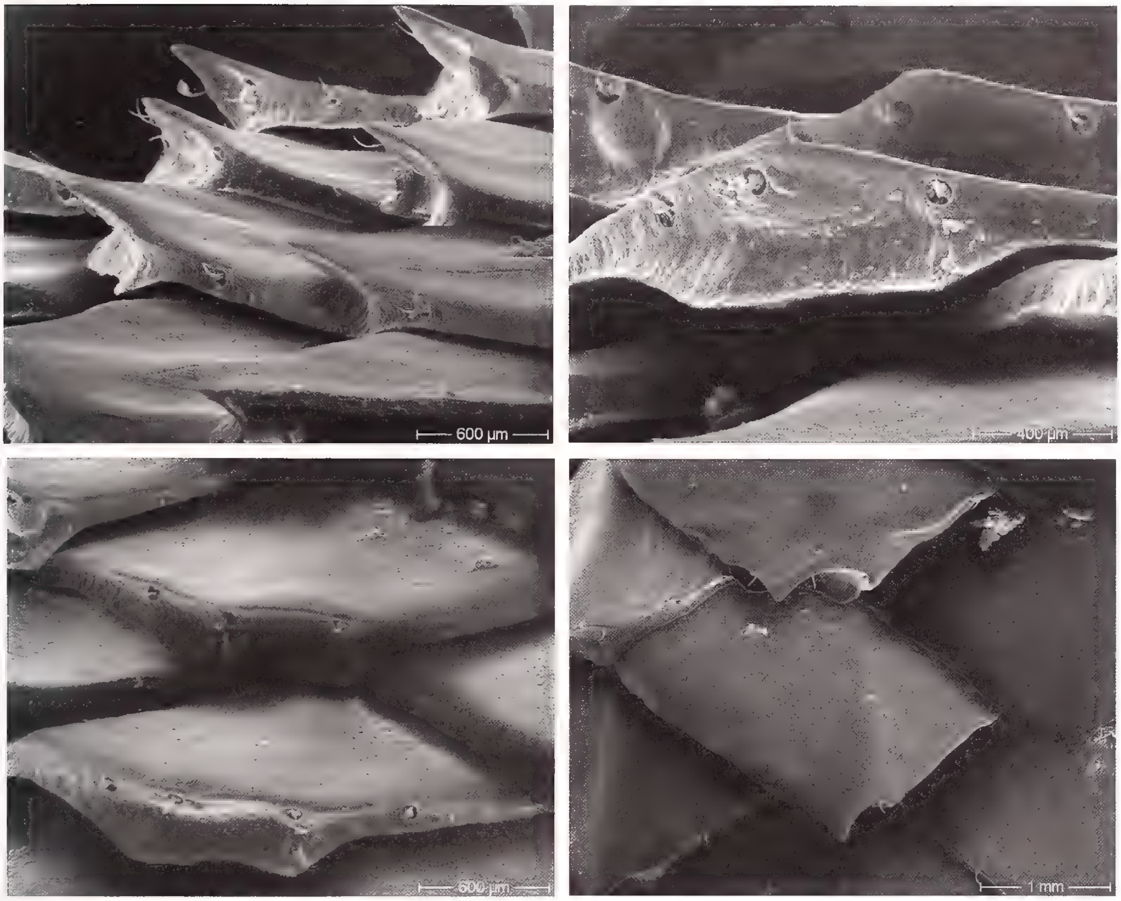


Fig. 6c. Neotype of *Lacerta agama* Linnaeus, 1758 (ZFMK 15222): SEM images of dorsal scales. Location of the scales is indicated by an arrow in fig. 6a.

Description of *Lacerta agama* Linnaeus, 1758

Agama agama (Linnaeus, 1758)

1734 *Salamandra americana* Seba, Naturalium Thesauri, thes. 1, Tome 1, Pl. 107, fig. 1–3.
1749 *Lacerta amphibia* Linnaeus, Amoenitates academicæ, vol. 1: 288.
1754 *Lacerta amphibia* Linnaeus, Museum Adolphi Friderici: 44.
1758 *Lacerta agama* Linnaeus, Syst. Nat., Ed. 10, 1: 207.
1802 *Agama colonorum* Daudin, Hist. Nat. gén. Part. Rept. 3: 358.
1831 *Agama occipitalis* Gray, in Griffith, Animal Kingdom Cuvier, 9 Synops. Spec.: 56.
1844 *Tropidolepis africanus* Hallowell, Proc. Acad. Nat. Sci. Philadelphia 1844: 171. Type locality: Liberia.
1877 *Agama colonorum* var. *congica* Peters, M. Ber. K. preuß. Akad. Wiss. Berlin. 1877: 612.
1877 *Agama picticauda* Peters, M. Ber. K. preuß. Akad. Wiss. Berlin. 1877: 612.
1884 *Agama agama savattieri* Rochebrune, (synonym of *A. a. africana* fide Grandison 1968) Faune Sénégambie, Rept.: 89.
1896 *Agama smithii* Boulenger, (fide Largen & Spawls 2006), Proc. zool. Soc. London 1896: 213.
1940 *Agama boensis* Monard, Arq. Mus. Bocage, Lisboa 11: 155. Type locality: Madina Boé, Guinea.
1957 *Agama agama mucosoensis* Hellmich, Veröff. Zool. Staatsamml. München 5: 44. Type locality: Dondo, Angola.

Neotype. ZFMK 15222: Mokolo, Margui-Wandala Province, northern Cameroon, leg. W. BÖHME & W. HARTWIG, 14.II.1974 (figs 6a–c).

Diagnosis. A large species of the genus. The nuptial male of *Agama agama* is characterized by a yellow head, a red throat and a tri-coloured (yellow, red and black) tail. The subordinate males, females, and adolescents possess an olive-green head and an olive-green to brown body with yellow dots, ocelli and stripes.

Description of the neotype of *Lacerta agama* Linnaeus, 1758

Adult male, measuring 290.11 mm in length (snout-vent length 128.93 mm, tail 161.18 mm, head length 33.49 mm, head width 23.61 mm, head height 14.07 mm).

Nostril slightly above the canthus rostralis, pierced in the middle of a large vaulted nasal scale, directed obliquely posterodorsally. Between the nostrils is a longitudinal, finely keeled shield, followed by finely keeled to smooth, regularly arranged scales in the interorbital region and on the remaining upper side of head. Supraocular scales are smooth. Parietal shield more or less pentagonal, parietal organ slightly visible. Nine supralabial scales on the left, eight on the right side, nine infralabial scales on both sides. The scales originating from both sides of the parietal midline have their imbrications anteriorly directed; the keels in the upper temporal region have their mucrones at the anterior margins. Ear-opening large, about the same size as the eye; tympanum visible; anterior margin being composed of spiny, mucronate scales. Four spiny tufts on the left side and five on the right, one before the ear opening, one above, one to two below and one to two behind. Nuchal crest low, consisting of 13 weakly differentiated lanceolate scales. Gular scales flat, juxtaposed and becoming smaller towards the gular fold. Dorsal scales keeled, becoming larger from neck and tail to the middle of the body; in 58 scale rows around midbody. Scales on tail arranged in weakly but nonetheless distinctly differentiated whorls that consist of three scale rings each, dorsally strongly, ventrally weakly keeled to smooth. Ventral scales smooth, slightly to strongly imbricate at their posterior margin; in 80 rows between throat and vent. One row of 10 preanal pores. Scales on forelimb with strongly keeled scales, on the upper arm twice as large as the dorsals, becoming smaller towards the underside and the manus. 3rd and 4th finger longest, 4th slightly longer, digital length decreasing 2–5–1, subdigital lamellae keeled. Hindlimbs also covered by distinctly keeled scales, on the upper tights twice as large as the dorsals, becoming larger towards the lower tights and smaller towards the underside.

Colouration in life. Head and nape reddish, limbs and body blue, base of tail white, followed by red and then black.

Remarks. The rank of the two subspecies *boensis* and *mucosoensis* is questionable. GRANDISON (1968) mentioned *boensis* as a large-scaled *Agama* species and therefore some vouchers from Guinea could be identical with that taxon and in this consequence *boensis* should be elevated to species rank (WAGNER & INEICH unpubl. data). *Agama a. mucosoensis*, with its striking blue and yellow colouration is as different to *A. a. agama* as *A. planiceps*, *A. lionotus* and many more well diagnosed species of the genus. Therefore it is very doubtful that *mucosoensis* is a subspecies of *agama*.

Acknowledgements. We are grateful to Pierre Andre Crochet for his advises using the International Code on Zoological Nomenclature and to Sven Kullander for using the images of the NRM specimens. Cornelius de Haan and Arie van der Pas translated the Dutch part of the text in Seba.

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A record of Asian agama of the genus *Calotes* Cuvier, 1817 (Squamata: Agamidae) in Kenya

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Abstract. Agamas of the genus *Calotes* Cuvier, 1817 occur in South and Southeast Asia. The garden lizard, *Calotes versicolor* (Daudin, 1802), was introduced or dragged to several places and islands in Asia, Indian Ocean and USA (Florida). The record of this species in Africa was regardless unexpected. We demonstrate the first record of *Calotes versicolor* in the African continent. Besides recognizing this species from the photograph, we were also able to identify it by using DNA sequencing.

Key words. *Calotes versicolor*, invasive species, African herpetofauna, distribution.

INTRODUCTION

Agamas of the genus *Calotes* Cuvier, 1817 occur in South and Southeast Asia (Moody 1980, Manthey & Schuster 1996). The garden lizard, *Calotes versicolor* (Daudin, 1802), is widespread in South and Southeast Asia. Its area of distribution extends from Southeastern Iran and Afghanistan to Nepal, India, Sri Lanka, Myanmar, Indo-China, Southern China, Malaysia and Sumatra (Manthey & Schuster 1996, Radder 2006). This species probably colonized Sri Lanka thanks to human settlers and became more abundant in areas with extremely disturbed vegetation (Erdelen 1984).

There are many regions or places in Asia and in the Indian Ocean where *Calotes versicolor* has been introduced or dragged. These are e.g.: Sumatra (Rooij 1915), Réunion and Mauritius (Vinson & Vinson 1969), Celebes (Erdelen 1978), the Maledives (Hasen Didi 1993), Oman (Seufer et al. 1999) and the Seychelles (Matyot 2004). Finally, the garden lizard has also been introduced to Florida in the USA (Enge & Krysko 2004). This species is adaptable and has a potential to be an invasive species with negative ecological impacts in the areas where it has been dragged (Matyot 2004; Radder 2006).

RECORD, METHODS AND RESULTS

Locality: Mombasa, railway station (GPS: S 04°03´27´´ E 039°39´37´´, 20 m a.s.l).

The first find was made on March 11, 2007 about 11 p.m. The individual, a female, was sitting on a metal container approx. 80 cm above the ground. The agama was caught, photographed (Fig. 1 and 2), and a sample for a DNA analysis was taken using buccal swabs.

Another observation was done during a short excursion on March 21, 2007 (about 6 p.m.). As previously, a single individual was sitting on a heap of old metal railway ties (Fig. 3) approx. 100 m from the first finding. Theoretically, this individual might have been the same as the first one. Its capture was unsuccessful and further identification was therefore impossible. The animal hid in the heap of ties. However, it was probably a female.

The railway station in Mombasa is situated close to the centre of the city. The territory of the station is fenced and guarded. The area of the station is several hectares large and its space is fragmented by used and unused buildings, wagons, containers, railroad ties, beams, planks, etc. The railway connects the railway station in Mombasa with the industrial port (Kilindini Harbour) distant by about one kilometer. The Mombasa railway station and port serve as a transship point for container transfer.

We also observed a second agama species at the Mombasa railway station. It was a member of the *Agama lionotus* complex. According to the referred occurrence (Spawls et al. 2004, Böhme et al. 2005) it could be *A. l.*

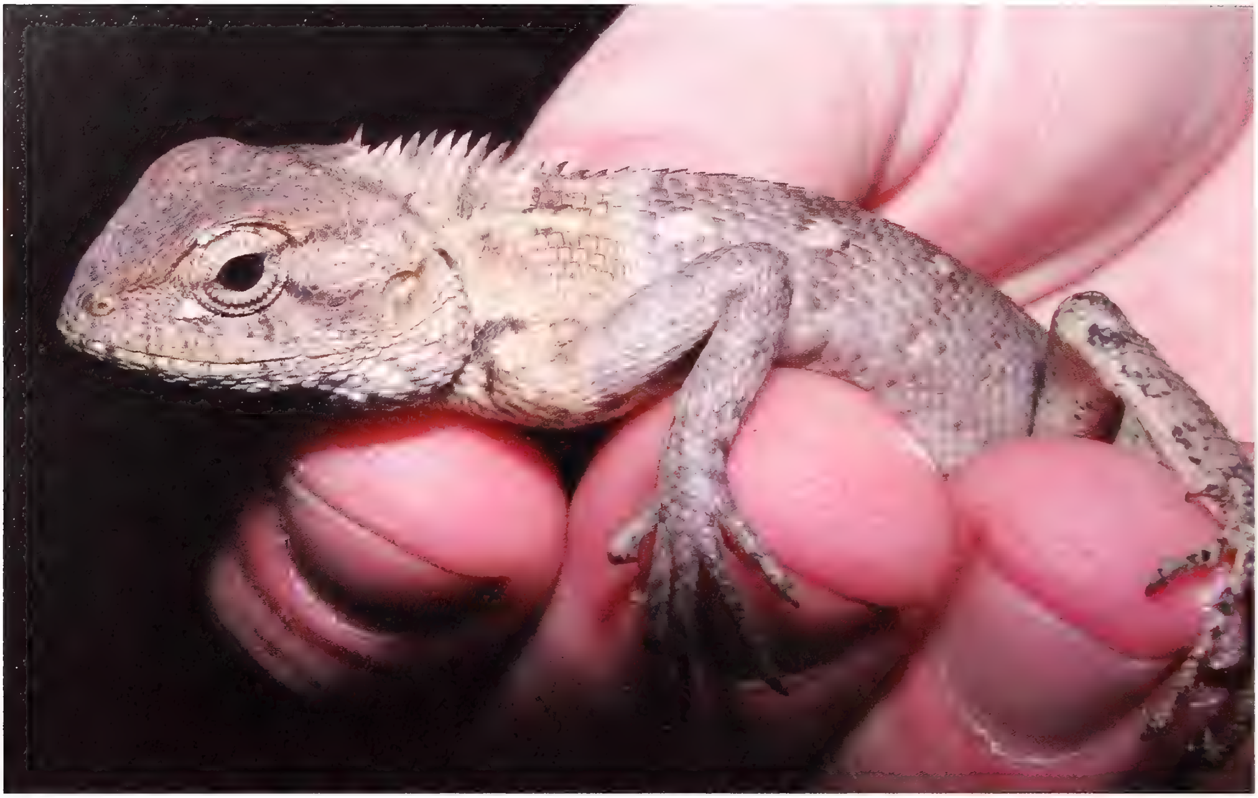

Fig. 1. *Calotes versicolor* from the Mombasa railway station. (11. III.2007; photo M. Lazurková).

lionotus. We saw males, females and offspring. We have also observed one gecko *Hemidactylus* cf. *platycephalus* and one specimen of *Hemidactylus* sp.

DNA was extracted from the buccal swab using NucleoSpin Tissue kit (Macherey-Nagel) following the manufacturer's protocol for buccal swabs. Fragments of mitochondrial cytochrome b gene and nuclear oocyte maturation factor mos (c-mos) gene were amplified by polymerase chain reaction using primers for cytochrome b from BURBRINK et al. (2000) and primers designed by SAINT et al. (1998) for c-mos. The sequencing was done with the same primers in the Abi Prism 3100 Avant Genetic Analyzer using the Abi Prism BigDye Terminator v 3.1 Ready Reaction Cycle Sequencing Kit (Applied Biosystems) in the sequencing laboratory of Charles University in Prague, Czech Republic. The obtained partial 420 bp sequence of c-mos gene was 99% identical with the sequence of c-mos gene of *Calotes versicolor* from GenBank (Acc. No. AF137525). We were unsuccessful in amplification of the whole mitochondrial gene for cytochrome b; however, two unambiguously sequenced fragments of this gene (245 bp and 364 bp) were identical with the cytochrome b sequence of *Calotes versicolor* from GenBank (Acc. No. AB183287) in 82 % and 84 %, respectively.

DISCUSSION

Based on the comparison of DNA from our sample and sequences published in GenBank, we can, with high confidence, confirm finding individuals of *Calotes versicolor* in Kenya. The lower correspondence in sequence composition in the cytochrome b gene might be explained by a faster rate of evolution of this fragment and the existence of multiple cryptic species in the *Calotes versicolor* group, as described previously by ZUG et al. (2006), who however used another fragment of mitochondial DNA.

The finding of one or two individuals of *Calotes versicolor*, although within a short time period, suggests a recent introduction. With regard to the proximity of the Kilindini Harbour the introduction was probably accomplished through shipping. The question is from which country the animals originate. Thanks to the lower correspondence in sequence composition in the cytochrome b gene mentioned above we can exclude Myanmar. The specimens from Mombasa presumably look like the specimens from islands Réunion and Mauritius (W. DENZER, Oxford, pers. comm. 2008).

Further faunistic research in Mombasa, namely at the railway station and the port, would be useful for a surveil-

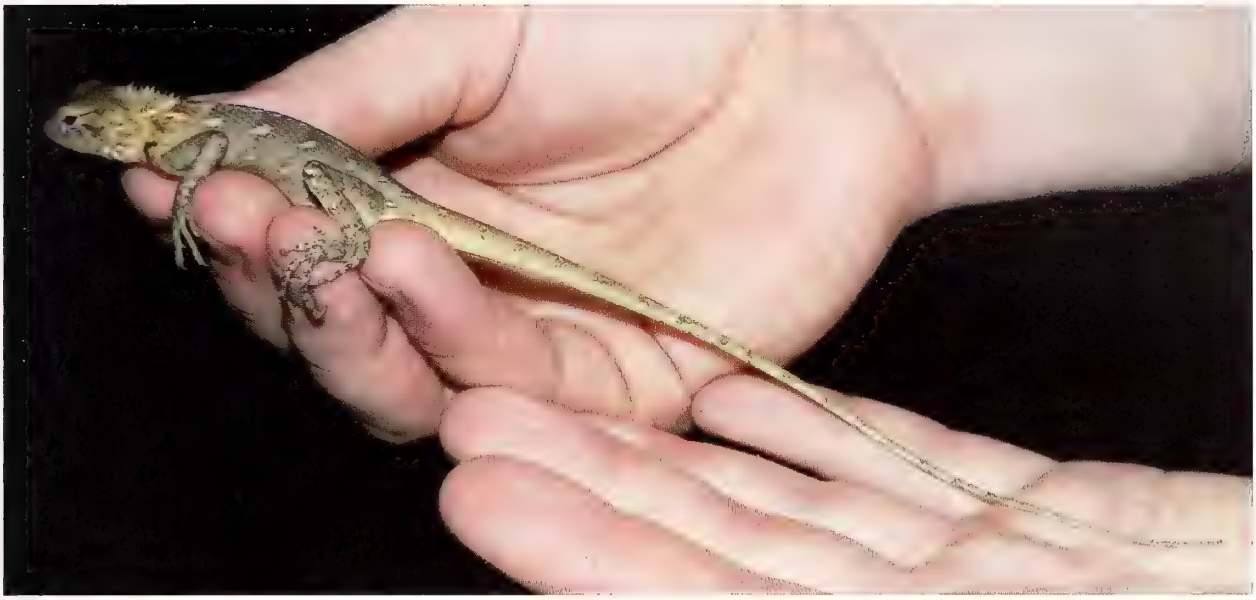

Fig. 2. *Calotes versicolor* from the Mombasa railway station. (11. III.2007; photo H. Šanderová).

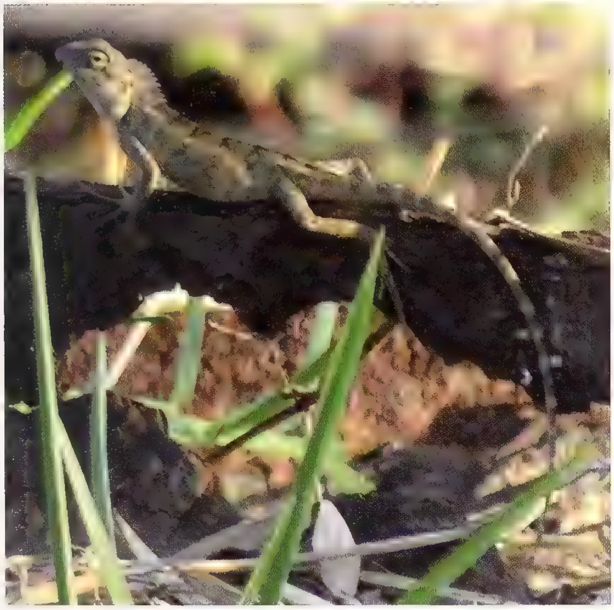

Fig. 3. *Calotes versicolor* from the Mombasa railway station. (21. III.2007; photo M. Šandera).

lance of the potential population of the *Calotes* agamas in Kenya. Their impact on the local herpetofauna (namely on other lizards) and on invertebrate fauna should also be investigated. The garden lizard could represent an invasive species in Kenya with negative ecological impacts. DIONG et al. (1994) have pointed out to the fact that in Singapore it has somewhere displaced the native *Bronchocela cristatella*. MAUREMOOTOO et al. (2003) include *C. versicolor* in the list of introduced vertebrates with a significant impact on native biodiversity in Mauritius, namely geckos, and consumes native invertebrates. VINSON (1968) assumed that *C. versicolor* may have been responsible for the disappearance or decrease of phasmids in Réunion and Mauritius.

Similar findings of introduced or dragged *Calotes versicolor* from other countries can also be expected in other places beside Africa.

Acknowledgements. We thank H. Šanderová and M. Lazurková for providing us with photographs. The travel to Kenya was supported from the Museum of Nature Bohemian Paradise, and DNA analysis together with the symposium De Agamis costs were covered by the Research Plan of the Ministry of Education, Youth and Sports of the Czech Republic 0021620828.

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Taxonomic and biological study on *Calotes ceylonensis* Müller, 1887 (Reptilia: Agamidae) of Sri Lanka

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Abstract. *Calotes ceylonensis* Müller, 1887 is an endemic, rare and vulnerable, arboreal agamid lizard species of Sri Lanka, which is found only at the low country dry and intermediate zones below 500 m a.s.l. This work is mainly based on examination of type specimens as well as published literature and our observations of ecological and conditions and threats on *Calotes ceylonensis*. The analysis of habitat data has shown that this species is widely spread within the well shading riverine-forested areas and poorly in the home gardens. The results of this survey indicate that *C. ceylonensis* lays about 4–12 eggs from August to October. Hatchlings come out from November to December. These lizards' natural predators are arboreal Colubrid snakes, Hornbills and Civet cats. The current habitat destruction poses a huge threat to this species.

Keywords. Agamidae, *Calotes ceylonensis*, Taxonomy, Natural history, Ecology, Biology, Behaviour, Sri Lanka.

INTRODUCTION

There are eighteen species of agamid lizards in Sri Lanka and fifteen (83.33%) of them are endemic to the island (DE SILVA 2006; MANAMENDRA-ARACHCHI et al. 2006). These eighteen species are classified under sub family Draconinae (MACEY et al., 2000). According to BAHIR & SURASINGHE (2005), MANAMENDRA-ARACHCHI et al. (2006) and IUCNSL & MENR (2007) four species are Critically Endangered; five species Endangered; three species Vulnerable and six Least Concern. The genus has a pit or fold in front of shoulder or none; body is compressed; supra ocular scales generally enlarged; dorsal scales are usually regular; dorsal crest and gular sac are more or less developed; tail is elongated, slender and sub cylindrical (DERANIYAGALA 1953).

The genus Calotes extends throughout southern Asia, most of the East Indian Archipelago (TAYLOR 1953).There are seven species in the genus *Calotes*. Five of them (*C. ceylonensis* Müller, 1887; *C. liocephalus* Günther, 1872; *C. liolepis* Boulenger, 1885; *C. nigrilabris* Peters, 1860; *C. desilvai* Bahir & Maduwage, 2005) are endemic to Sri Lanka. The remaining two *Calotes* species (*C. calotes* [Linnaeus, 1758]; *C. versicolor* [Daudin, 1802]) are probably widespread throughout South East Asia. According to the published literature *Calotes ceylonensis* is a largely arboreal species found only from the low country dry and intermediate zones below 500 m a.s.l (DAS & DE SILVA 2005; MANAMENDRA-ARACHCHI & LIYANAGE 1994). Its conservation status is Rare and Vulnerable (MANAMENDRA-ARACHCHI & LIYANAGE 1994; IUCNSL & MENR 2007). The information available on this species is marginal, and therefore further studies on their behaviour and ecology, which may be very important for the conservation of the species, are needed. Hence it is essential to gather information on the *C. ceylonensis* in different areas of the country as a first step towards conservation of this lizard species.

MATERIALS AND METHODS

The material examined is deposited at the NMB, Naturhistorisches Museum Basel, Switzerland and WHT, Wildlife Heritage Trust of Sri Lanka, Colombo, Sri Lanka. Diagnoses and descriptions are based on external morphology. This work is mainly based on examination of type

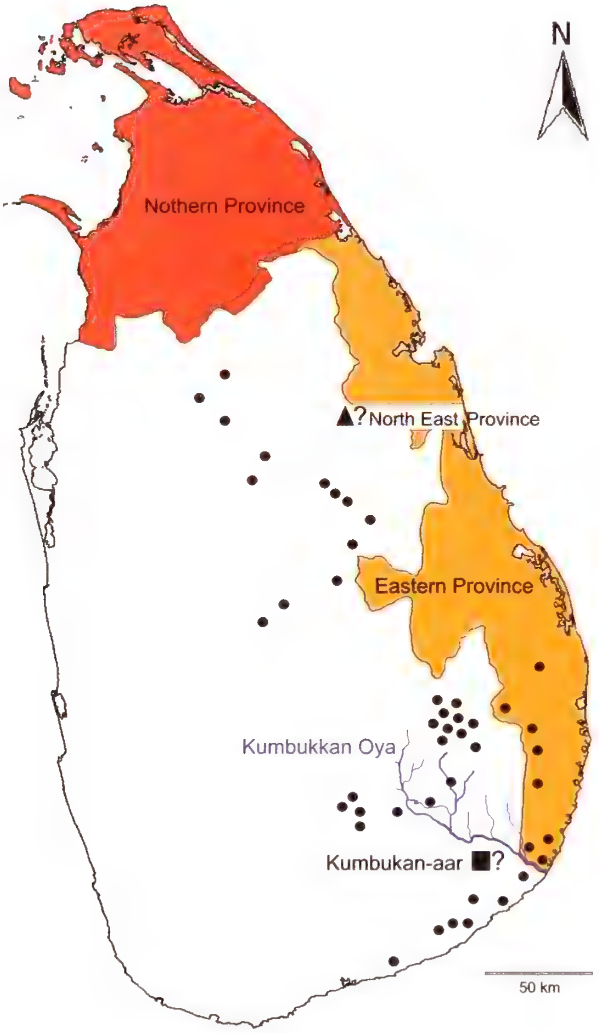

Fig. 1. Distribution map of *C. ceylonensis* (Square, Holotype; Triangle, Paratype; Circle, Other).

specimen and WHT specimens as well as published literature and our observations on their ecological and behavioural conditions and threats. The locality records for each species include WHT specimen data, published locality records as well as our observations during past decade. We have examined 45 localities (March 2002 to April 2006) throughout 7 districts (Anuradapura: 5 / Monaragala: 13 / Ampara: 8 / Hambantota: 7 / Badulla: 4 / Matale: 3 / Polonnaruwa: 5) (fig. 1). A total of 68 individuals (males: 37; females: 18; juveniles: 13) were recorded during the study period. The collected species were examined, measured and noted down carefully before released back to the same habitats (tab. 1 & 2). The diagnostic keys given by DERANIYAGALA (1953), MANAMENDRA-ARACHCI (1990), MANAMENDRA-ARACHCI (1998), MANAMENDRA-ARACHCHI & LIYANAGE (1994), SMITH (1935) and TAYLOR (1953) were used for species identification. Principal components analysis of preferred habitats was done using Pcord4 and each number of males, females and juveniles against the preferred habitat type were used in this analysis.

All the photographs and line drawings displayed with the photographer's and artist's initials; ES (Edi Stöckli), TA (Thasun Amarasinghe) and SK (Suranjan Karunarathna).

All measurements were taken to the nearest 0.1 mm with dial calipers.

Scale counts. **SUP**, Supralabials were counted from the first scale anterior to that at angle of gape, not including the median scale (when present); **INF**, infralabials were counted from first scale posterior to mental, to angle of gape; **DS**, dorsal spines were counted from first spine to last of mid-dorsal row; **CR,** canthus rostralis (counted from rostral scale along scale row passing over nostril to posterior end of supraciliary ridge); **MDS**, mid dorsal scales (counted from scale behind rostral to posterior margin of the thigh); **MBS,** mid body scales were counted from center of mid-dorsal row forwards and downwards across ventrals (this count is, however, made unreliable by the unequal size and uneven arrangement of the lateral scales); **MVS**, mid ventral scales were counted from first scale posterior to mental, to last scale anterior to vent; **SAT**, Spines around tympanum were counted from first spine to last above tympanum.

External measurements. **SVL**, snout–vent length (distance between tip of snout to anterior margin of vent); **HL**, head length (distance between posterior edge of mandible and tip of snout); **HW**, head width (maximum width of head); **DHL**, dorsal head length (distance between posterior edge

Table 1. Measurements of *C. ceylonensis* hatchlings.

	Measurement given in mm											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**Average**
SVL	34.1	32.8	35.0	34.5	34.6	35.1	33.9	34.8	33.4	34.2	32.9	34.11
TL	65.5	66.8	67.2	64.8	66.1	63.4	66.2	64.5	63.9	66.5	65.8	65.51

Table 2. Measurement of *C. ceylonensis* Eggs.

No.	Egg length	Egg width
1	16.5	8.6
2	16.8	8.4
3	14.3	7.9
4	15.6	8.5
5	15.2	8.7
6	17.1	8.8
7	16.9	7.8
8	17.1	7.6
9	14.6	8.5
10	15.7	7.8
11	14.8	7.9
12	14.4	8.3
13	15.5	8.8
14	16.1	8.9
15	16.7	7.9
16	16.2	8.5
17	13.8	8.1
18	14.5	8.6
19	15.3	8.4
20	13.9	8.1
21	13.5	8.9
22	17	7.9
23	16.8	8.3
24	16.4	8.7
25	15.8	8.1
26	15.5	8.8
27	13.6	7.9
28	13.5	8.6
29	15.3	8.9
30	16.7	7.8
31	16.2	8.3
32	16.6	8.8
Mean	**15.55**	**8.34**

of cephalic bone and tip of snout); **NFE**, nostril – front eye length (distance between most anterior point of orbit and middle of nostril); **UAL**, upper-arm length (distance between axilla and angle of elbow); **LAL**, lower-arm length (distance from elbow to wrist with both upper arm and palm flexed); **FL**, finger length (distance between tip of claw and the nearest fork); **FEL**, femur length (distance between groin and knee); **TBL**, tibia length (distance between knee and heel, with both tibia and tarsus flexed); **TL**, toe length (distance between tip of claw and nearest fork); **AG**, axilla–groin length (distance between axilla and groin); **SA**, snout–axilla length (distance between tip of snout and axilla); **TAL**, tail length (measured from anterior margin of vent to tail tip); **PAL**, palm length (taken from posterior most margin of palm and tip of longest finger); **FOL**, foot length (distance between heel and tip of longest toe, with both foot and tibia flexed); **TBW**, width of tail base (most distance of the tail base); **IOW**, inter orbital width (least distance between the upper margins of orbits); **ED**, eye diameter (horizontal diameter of orbit); **SFE**, snout–front eye length (distance between anterior most point of orbit and tip of snout); **SBE**, snout–back eye length (distance between posterior most point of orbit and tip of snout); **SFT**, snout–front tympanum length (distance between anterior most point of tympanum and tip of snout);**TD**, Tympanum diameter (least distance between the inner margins of tympanum).

RESULTS

***Calotes ceylonensis* Müller, 1887**
English Name: Painted-lip Lizard
Sinhala Name: Thola – wisithuru Katussa

Calotes mystaceus, var. ceylonensis Müller, 1887 (Müller 1887: 8, 292–293, pl. 3.).

Calotes ceylonensis (Boulenger 1890; Deraniyagala 1931; Smith 1935; Taylor 1953).

Calotes kelaartii Nevil, 1887 (Haly 1887: 2, 133. [Species described but not named]; Nevil 1887: 2, 134, pl. 5 [Species named but not described]).

Calotes saleoides Werner, 1896 (Werner 1896: 46, 7).

Holotype (fig.2). Male (81.9 mm SVL); *Cat. no.* NMB 3340; *Loc.* Kumbukan-aar: South East Ceylon (= Kumbukkan Oya?: Sri Lanka [“aaru” *in Tamil*= “Oya” *in Sinhala*]); *Coll.* P. Sarasin & F. Sarasin; *Date.* 1886.

Paratype (in NMB catalogue labeled as Syntype). Male

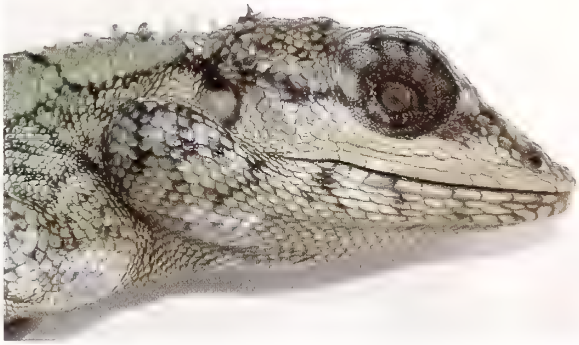

Fig. 2. *C. ceylonensis,* NMB 3340; Holotype, male; lateral aspect of head (ES).

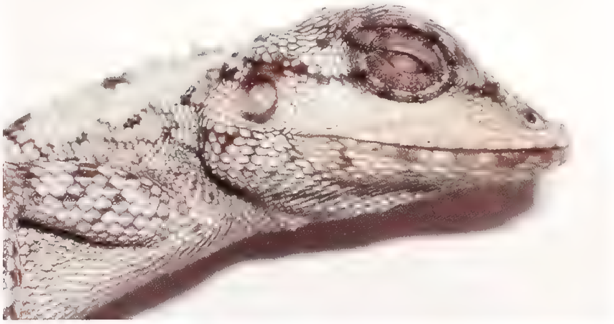

Fig. 3. *C. ceylonensis,* NMB 3341; Paratype, male; lateral aspect of head (ES).

(67.6 mm SVL); *Cat. no.* NMB 3341; *Loc.* North East province: Ceylon (= Northern Province ? / Eastern Province ?: Sri Lanka); the same coll. & same date (fig. 3).

Other materials examined. WHT 7397, male, 59.1 mm, Wasgamuwa; WHT 7514, male, 74.8 mm, Giritale; WHT 1427A, male, 79.6 mm, Wasgamuwa; WHT 1427B, male, 75.0 mm, Wasgamuwa; WHT 1427C, female, 76.7 mm, Wasgamuwa; WHT 1427D, female, 61.6 mm, Wasgamuwa; WHT 1428, male, 80.3 mm, Tatugala-Bulupitiya; WHT 0515, male, 72.9 mm, Pallegama; WHT 1625A, male, 77.2 mm, Wasgamuwa; WHT 1625B, male, 71.9 mm, Wasgamuwa; WHT 0511, male, 82.5 mm, Konketiya-Buttala; WHT 0521, female, 72.1 mm, Konketiya-Buttala; WHT 0522, male, 73.2 mm, Konketiya-Buttala; WHT 0519, male, 73.0 mm, Yala; WHT 0520, male, 73.4, Yala. WHT 1624A, male, 65.1 mm, Wasgamuwa

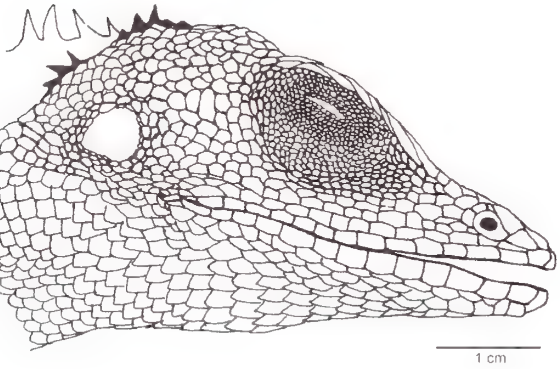

Fig. 4. *C. ceylonensis,* WHT 0511; male; lateral scalation of head (TA).

Diagnosis. Two well-separated spines above the tympanum, the anterior and upper lateral pointing backwards and upwards, the other straight backwards, an oblique fold in front of the shoulder runs across throat covered with small granular scales. Dorsal crest formed of 7 to 13 small spines. In a fully-grown male the head is larger and the base of the tail more swollen.

Description. (Based on MÜLLER 1887; Holotype (NMB 3340); Paratype (NMB 3341) and WHT collection). Length of head one and a half times its breadth; snout a little longer than the orbit; forehead concave; cheeks swollen in the adult male; upper head scales unequal, smooth; canthus rostralis and supraciliary edge sharp; two well separated spines above the tympanum, the upper and anterior one mid way between it and the nuchal crest; diameter of the tympanum half that of the orbit; Supralabials, 10–14; Infralabials, IX–XIII (fig. 4). Body compressed; dorsal scales rather small, smooth or faintly keeled, the anterior and upper ones pointing backwards and upwards (fig. 5); the others straight backwards, larger than the ventrals, which are strongly keeled and mucronate; 53 to 76 scales round the body. No trace of a gular sac; gular scales strongly keeled, as large as the ventrals; an oblique fold in front of the shoulder runs across throat covered with small granular scales. Dorsal crest

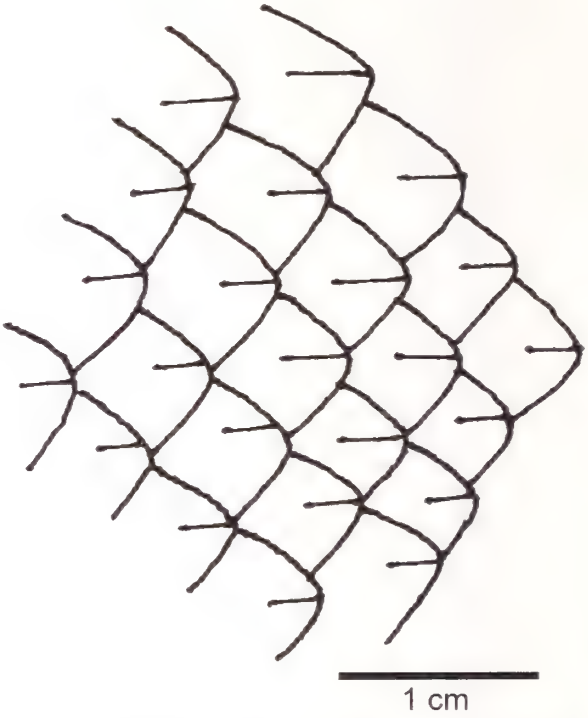

Fig. 5. *C. ceylonensis,* WHT 0511; male; mid body lateral scales (TA).

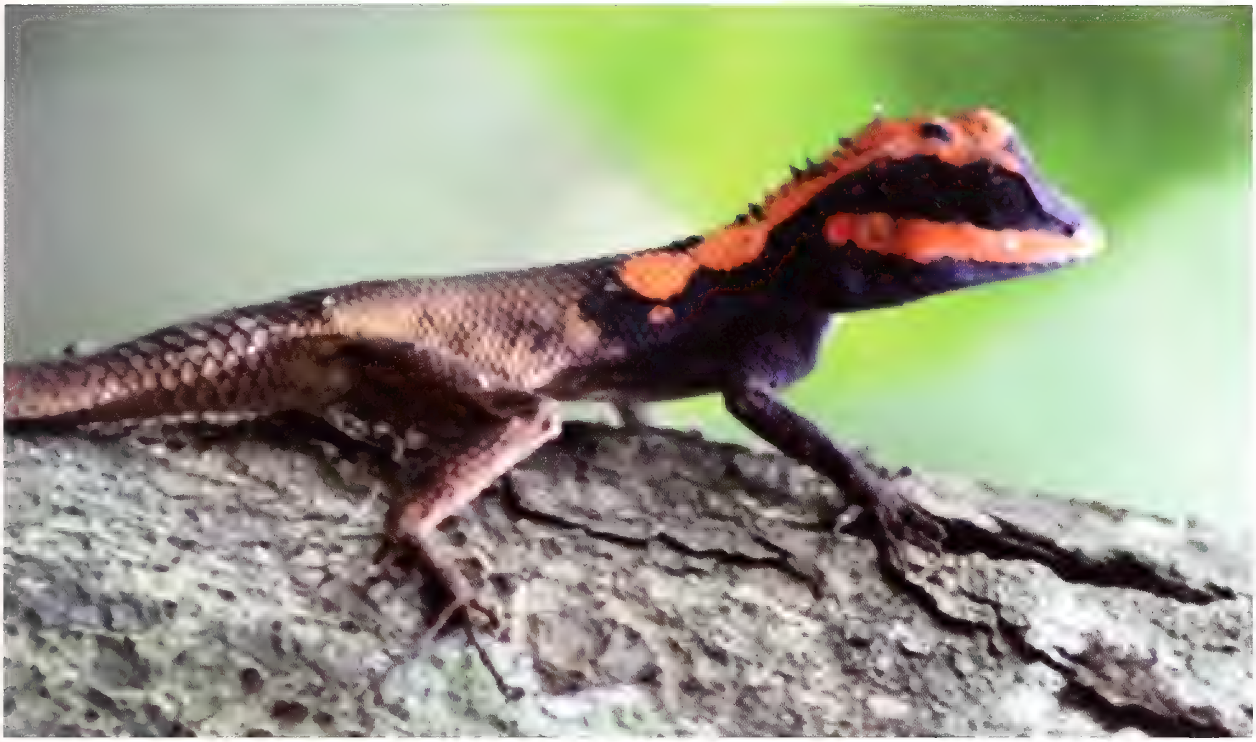

Fig. 6. *C. ceylonensis* Mature Male (lateral aspect) (SK).

formed of 7 to 13 small spines; no dorsal crest. Limbs moderate; third and fourth fingers are sub equal; Relative length of fingers; 1<5<2<4<=3. Fourth toe distinctly longer than third. Relative length of toes; 1<2<5<3<4. The hind limb reaches to the tympanum or beyond. Tail long and slender; in the adult male it is markedly swollen at the base, with large, thick, keeled scales, those of the upper median row forming a slight serrated ridge.

Remarks. (Based on Müller [1887] and observations on living specimens). The body color is changeable from grayish brown to light blue or dark brown, back of the head and anterior part of back pale brownish, divided in to more or less distinct spots by dark transverse bars; hinder part of back and tail with dark cross bars; upper lip with a pale strongly defined stripe, which extends to beyond the ear; sides of neck and chest black or white with black reticulations; gular region grayish or blackish; belly pale brown with more or less distinct angular bands (figs. 6 & 7).

Scale counts and External measurements (in mm) **of Holotype.** SUP, 10; INF, 10; DS, 9; CR, 14; MBS, 59; MDS, 78; MVS, 101; SAT, 2; SVL, 81.9; HL, 31.2; HW, 18.6; DHL, 20.6; NFE, 6.7; UAL, 12.3; LAL, 14.7; FLI, 4.3; FLII, 7.0; FLIII, 10.1; FLIV, 9.6; FLV, 6.6; FEL, 20.3; TBL, 22.7; TLI, 4.2; TLII, 7.5; TLIII, 11.6; TLIV, 14.1; TLV, 9.9; AG, 33.9; SA, 37.7; TAL, 185; PAL, 12.2; FOL,

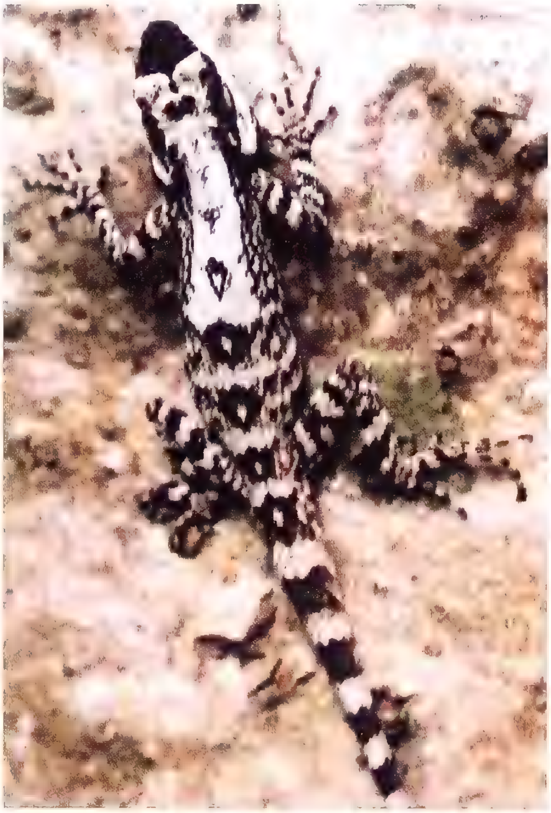

Fig. 7. *C. ceylonensis* Mature Male (dorsal aspect) (TA).

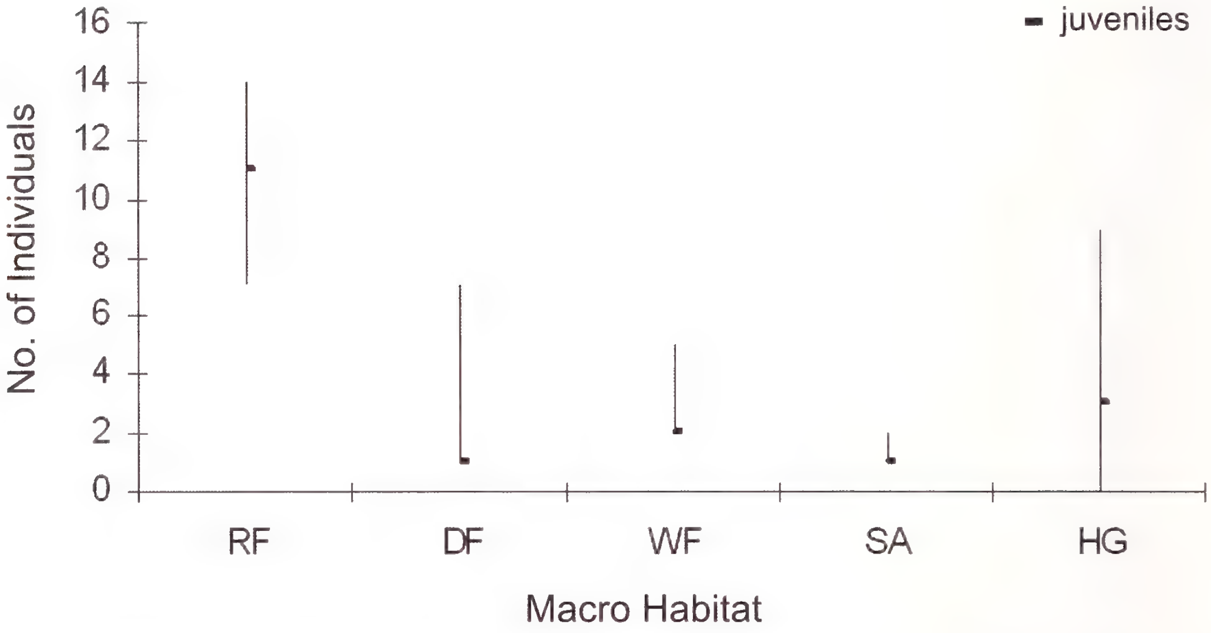

Fig. 8. PC analysis of preferred macro habitats (RF, Riverine Forests; DF, Dry-mixed Forest; WF, Wet-mixed Forest; SA, Savannah; HG, Home Gardens).

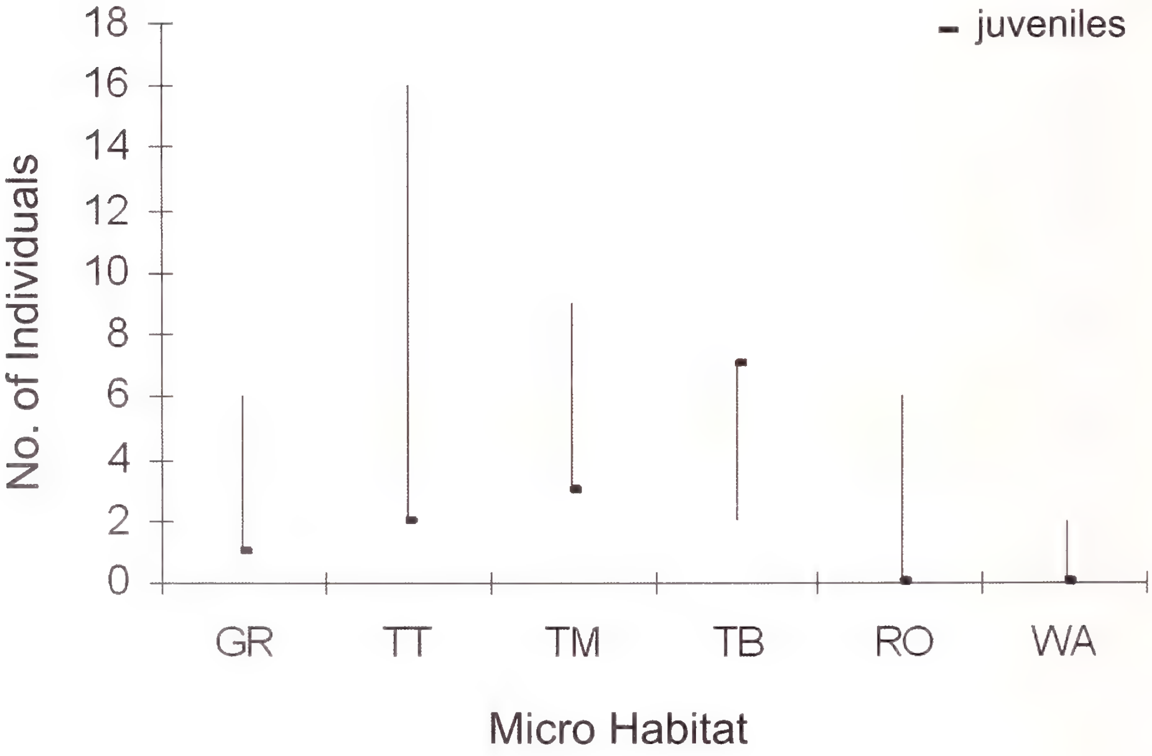

Fig. 9. PC analysis of preferred micro habitats (GR, Ground; TT, Tree Top - >10m height; TM, Middle of Tree 5 to 10m height; TB, Base of Tree 1 to 5m height; RO, On Rocks; WA, On Walls).

22.2; TBW, 10.2; IOW, 12.4; ED, 8.3; SFE, 10.8; SBE, 18.8; SFT, 23.5; TD, 2.8.

Scale counts and External measurements (in mm) **of Paratype.** SUP, 11; INF, 11; DS, 8; CR, 14; MBS, 53; MDS, 73; MVS, 84; SAT, 2; SVL, 67.6; HL, 19.9; HW, 11.6; DHL, 16.2; NFE, 4.7; UAL, 9.7; LAL, 11.2; FLI, 4.0; FLII, 6.4; FLIII, 7.5; FLIV, 7.3; FLV, 5.1; FEL, 16.3; TBL, 16.0; TLI, 3.5; TLII, 6.0; TLIII, 10.2; TLIV, 10.6; TLV, 8.6; AG, 27.5; SA, 25.1; TAL, 156; PAL, 10.6; FOL, 17.9; TBW, 6.3; IOW, 9.0; ED, 6.0; SFE, 8.1; SBE, 13.5; SFT, 11.6; TD, 2.6.

Distribution and Habitat. *Calotes ceylonensis* is recorded only from the semi evergreen monsoon forests, plantations and home gardens of the dry and intermediate zones up to 500 m a.s.l. within the well shading riverine-forested areas and poorly in the home gardens (Das & De Silva 2005; Erdelen 1984; Manamendra-Arachchi & Liyanage 1994). According to our observations a large number of individuals of this species mostly favour shady riverine forests over the other macro habitats (fig. 8) and we also could locate a great number of individuals from top of the trees rather than the other microhabitats (fig. 9).

According to our survey the female sex ratio is low comparatively to the males except in Ampara district. The highest number of males was recorded from Monaragala district and least numbers from Matale and Badulla districts and also the number of females, juveniles, hatchlings as well as eggs were low in these two districts (fig. 10 and tab. 3).

Reproduction. There have been only few attempts to use hemipenis morphology as a taxonomic tool for agamid lizards although there is a considerable amount of structural diversity (McCann 1949, Böhme 1988). The hemipenis of *C. ceylonensis* (fig. 11) seems less differentiated as compared to *C. nigrilabris* and *C. liocephalus* (see also the descriptions and fig. 18 in Böhme 1988). The pedicel is considerably longer than the head; below the head, it is broadened out in to two shallowly concaved shoulders; there are no spines. The head is quadrangle in shape. It is shallowly divided longitudinally in to four lobes, two being very slightly larger than the others. The surface of the head is reticulatedly pitted, the pits being larger on the outside and diminishing in size towards the divisions between the lobes (fig. 11).

The female digs a nest hole in the ground and deposits about 4–12 eggs in August to October on shady places near from tree bases. While laying eggs the females change their body color to black. The eggs are 13.5 mm–17.1 mm long and 7.8 mm–8.9 mm wide. Hatchlings come out from November to December (Deraniyagala 1953).

Behaviour. This species is largely arboreal and active during the day, widely spread within the well shading riverine-forested areas and poorly in the home gardens. They

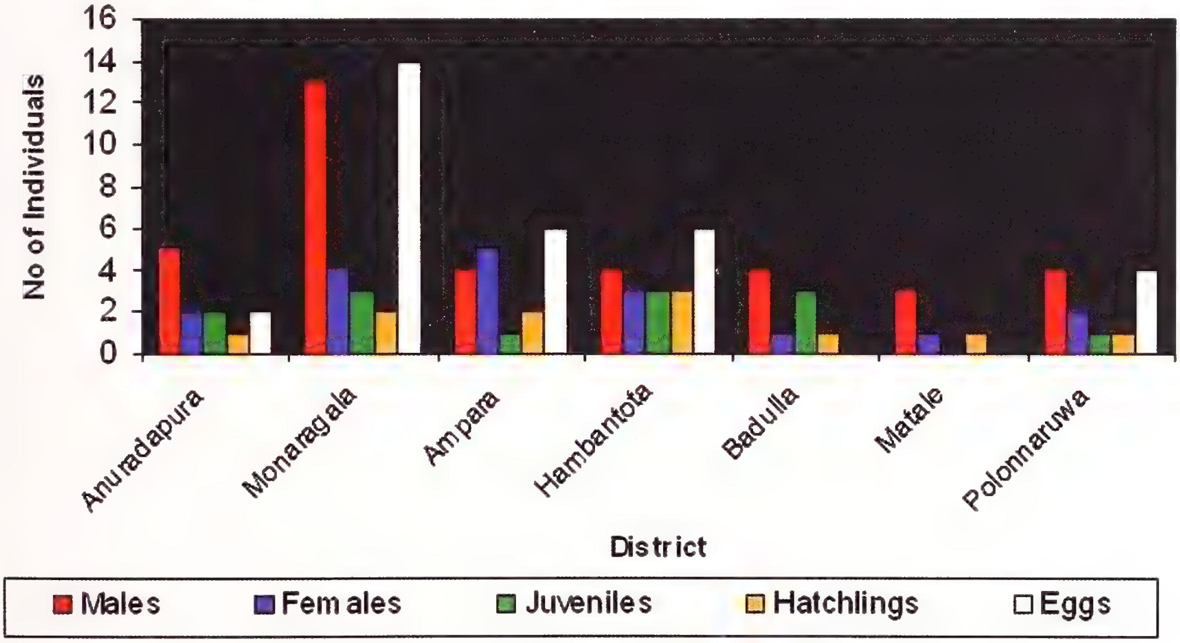

Fig. 10. No. of individuals recorded in each district.

Table 3. Observed locations and individual details of *C. ceylonensis*.

District	Location	No. of Males	No. of Females	No. of Juveniles	No. of Eggs	No. of Hatchlings
Monaragala	Pitakumbura	1	0	1	2	1
	Wellavaya	1	1	0	0	0
	Puwakpale	1	0	0	2	0
	Bulupitiya	1	1	0	2	0
	Monaragala	1	0	1	2	0
	Hangala	0	1	0	0	1
	Yakunhela	0	0	0	0	0
	Buttala	1	0	0	2	0
	Nilgala	3	1	0	0	0
	Ulhela	1	0	1	2	0
	Rathugala	1	0	0	2	0
	Pihibiyamukalana	1	0	0	0	0
	Hamapola	1	0	0	0	0
Ampara	Hulannuge	0	1	0	2	0
	Buddangala	0	1	0	0	1
	Kumana	0	1	0	0	0
	Galoya	1	0	1	0	0
	Yala	1	1	0	0	1
	Makara	1	0	0	2	0
	Aravila	1	0	0	0	0
Hambantota	Manakanda	0	1	0	2	0
	Palatupana	0	1	0	2	1
	Kataragama	0	1	1	2	1
	Weeravila	0	1	0	2	0
	Hambantota	1	0	1	0	1
	Akasachihthiya	1	0	0	0	0
	Tissamaharama	1	0	0	0	0
	Yala	1	0	1	0	0
Polonnaruwa	Maduruoya	0	1	1	0	0
	Giritale	1	0	0	2	0
	Polonnaruwa	1	0	0	2	1
	Wasgomuwa	1	0	0	0	0
	Minneriya	1	1	0	0	0
Badulla	Koslanda	1	0	0	0	0
	Udadiyaluma	1	0	1	0	1
	Akkaraseya	1	1	1	0	0
	Nikapotha	1	0	1	0	0
Matale	Ilukkumbura	1	0	0	0	0
	Wasgomuwa	1	1	0	0	1
	Narangamuwa	1	0	0	0	0
Anuradapura	Galkulama	1	1	0	0	0
	Padaviya	1	0	1	0	0
	Ritigala	1	1	0	0	1
	Anuradapura	1	0	1	0	0
	Kekirawa	1	0	0	2	0

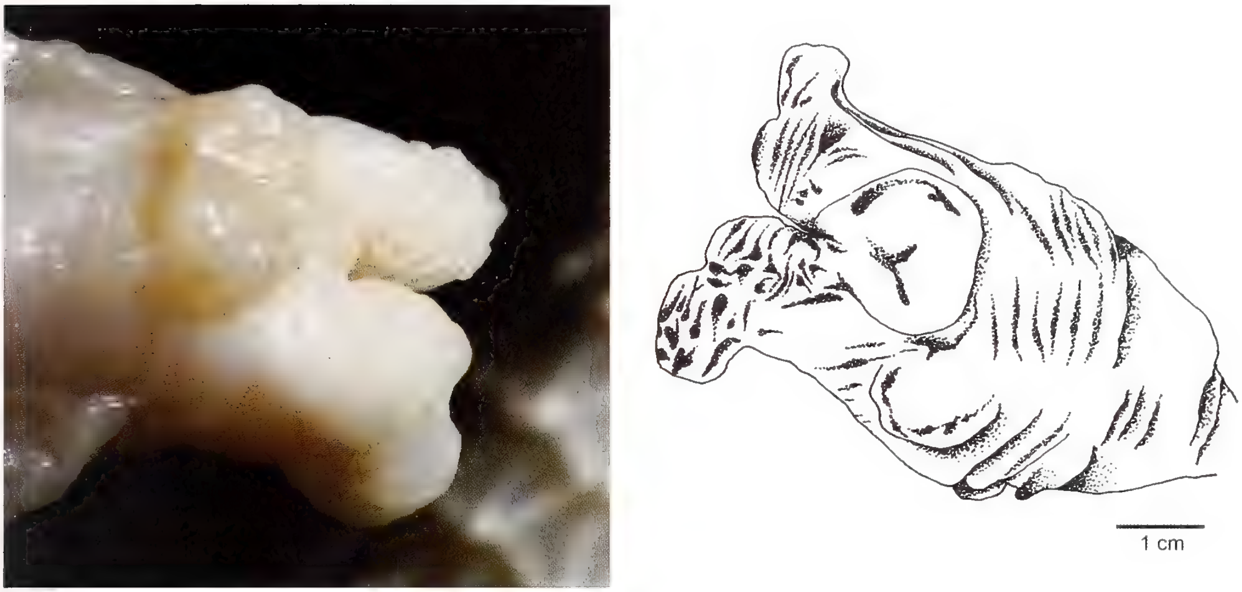

Fig. 11. *C. ceylonensis*, WHT 1428; male, 80.3 mm SVL; lateral aspect of left hemipenis (TA).

specially feed on butterflies, honeybees and other insects. These lizards' natural predators are arboreal colubrid snakes, hornbills and civet cats. Being in danger this lizard suddenly climbs into a tree to an average height of 15 m and then glides to another tree, which is 1 m away till the danger disappears. If there is no other tree to glide, they just jump down to the ground and stay a few minutes without moving, and then suddenly run on another tree. Hatchlings are mostly waiting for their preys on *Lantana camera* trees (an invasive plant to Sri Lanka) while camouflaging their snout color into pink (the flowers of *L. camera* are also pink). Their prey are insects which feed on *L. camera.*

Conservation status. Rare (Manamendra-Arachchi & Liyanage 1994), Least Concern (Bahir & Surasinghe 2005) and Vulnerable (Iucnsl & Menr 2007).

Discussion

The holotype of *Calotes ceylonensis* (NMB 3340) was collected from "Kumbukan-aar: South East Ceylon" by P. & F. Sarasin. Today there is known no area or river basin as "Kumbukan-aar" in South East Sri Lanka. However there is a river basin called "Kumbukkan Oya". In Sinhala "Oya" means a small river/large stream. In Tamil "aaru" is the same meaning for "Oya or River". There are several rivers in East and North parts of Sri Lanka named as "aaru" in Tamil. However there is no evidence that name used for "Kumbukkan Oya". Somehow the Tamil people live in that area used to call this river as "Kumbukkan aaru". Therefore we believe that the person who gave this information to P. & F. Sarasin might have been be a Tamil person. In addition now there is also a considerable population of *C. ceylonensis* inhibiting this area. Therefore we assume the name for holotype locality as "Kumbukkan Oya", which is currently used in Sri Lanka.

In addition the paratype of (NMB 3341), was collected from "North East province: Ceylon" by the same collectors. Actually nowadays there is no district as "North East province" in Sri Lanka and this province considered as two provinces called Northern Province and Eastern Province. Therefore it is difficult to place the exact location and also *C. ceylonensis* is distributed throughout these two provinces of the country.

The ecological and behavioural status of *C. ceylonensis* has not been investigated up to now. *C. ceylonensis* is an endemic, rare and vulnerable species. Therefore many published literature on their ecological status will have to be done for the conservation of this species. And also captive breeding methods may be needed for ex-situ conservation of these species. A major portion of the primary forests of Sri Lanka has undergone considerable destruction during the past 150 years. As a result: most of the agamid lizards that inhabit in these primary forests now live in degraded or altered habitats. According to De Silva (1996) *C. ceylonensis* is distributed in primary forest where a considerable amount of destruction and alteration of the forest by human activities have taken and are still taking place. As a consequence only 5% to 25% of primary or secondary forest / scrub jungle still exist with the greater extent being anthropogenic vegetations. *C. ceylonensis* is sympatric with *Calotes liolepis* in Ritigala, Nilgala, and the eastern slope of the Knuckles region; with *C. versicolor, Otocryptis nigristigma, Lyriocephalus scutatus* and *Sitana ponticeriana* in many habitats throughout the intermediate and dry zones.

Acknowledgements. We would like to express our sincere thank to Kelum Manamendra-Arachchi (WHT) and M. M. Bahir who provided valuable comments and helped improve the document. We also thank Rohan Pethiyagoda (WHT), Franz Tiedemann (NMW), Madhava Botegue (TNCS) and Sudath Nanayakkara (WHT), who helped in diverse ways to enrich this work.

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Studies on African *Agama* VI. Taxonomic status of the West African *Agama* (Sauria: Agamidae) with prominent tail crests: *Agama boulengeri* Lataste 1886, *Agama insularis* Chabanaud, 1918 and *Agama cristata* Mocquard, 1905

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Abstract. This publication reviews the taxonomy of three West African *Agama* species, *A. boulengeri*, *A. cristata*, and *A. insularis*, each characterized by a prominent tail crest in adult males. Following the results from morphological and genetic analyses, *Agama insularis* is recognized as a synonym of the revalidated *Agama cristata*, whereas this species is clearly distinct from *Agama boulengeri*. We present a detailed distribution map for these *Agama* species, as well as for *A. weidholzi*. Following the results of recent publications, *Agama atra knobeli* is herein regarded as a full species.

Key words. Africa, Guinea, Los Islands, Île de Roumé; Sauria, Agamidae, *Agama cristata*, *A. insularis*, *A. boulengeri*, *A. knobeli*, *Agama weidholzi*.

INTRODUCTION

Despite an increasing amount of work on the taxonomy and phylogeny of African lizards in the genus *Agama* (Böhme et al. 2005, Padial 2005, Wagner 2007, Wagner et al. 2008a, Wagner et al. 2008b, Wagner et al. 2009a, Wagner et al. 2009b) several species are only poorly known, and the validity of some taxa remains questionable (e.g. *A. bocourti* Rochebrune, 1884; *A. bottegi* Boulenger, 1897; *A. cornii* Scortecci, 1928; *A. insularis* Chabanaud, 1918 and *A. agama boensis* Monard, 1940 [regarded as a synonym of *A. weidholzi* by Grandison 1969]). Many species are only diagnosable based on adult male coloration (Loveridge 1933, Thys van den Audenaerde 1963, McLachlan 1981, Böhme et al. 2005, Wagner 2007, Wagner et al. 2008a, Wagner et al. 2008b), and the lack of appropriate comparative material coupled with inadequate descriptions of the adult coloration in life prevents formal taxonomic evaluations.

Three species in West Africa are characterized by possessing a prominent tail crest in adult males: *Agama boulengeri*, *A. insularis* and *A. cristata*. The taxonomic status of these taxa is the focus of this study.

Agama insularis, was described by Chabanaud (1918) on the basis of a juvenile and a subadult female collected by Dr. G. Bouet in 1914 on Île Roumé, which is part of the Îles de Los archipelago located in the Atlantic Ocean just several kilometres (ca. 8 km) offshore from Conakry, Guinea. In his description of *A. insularis,* Chabanaud (1918) only compared his new species with *Agama kirkii*

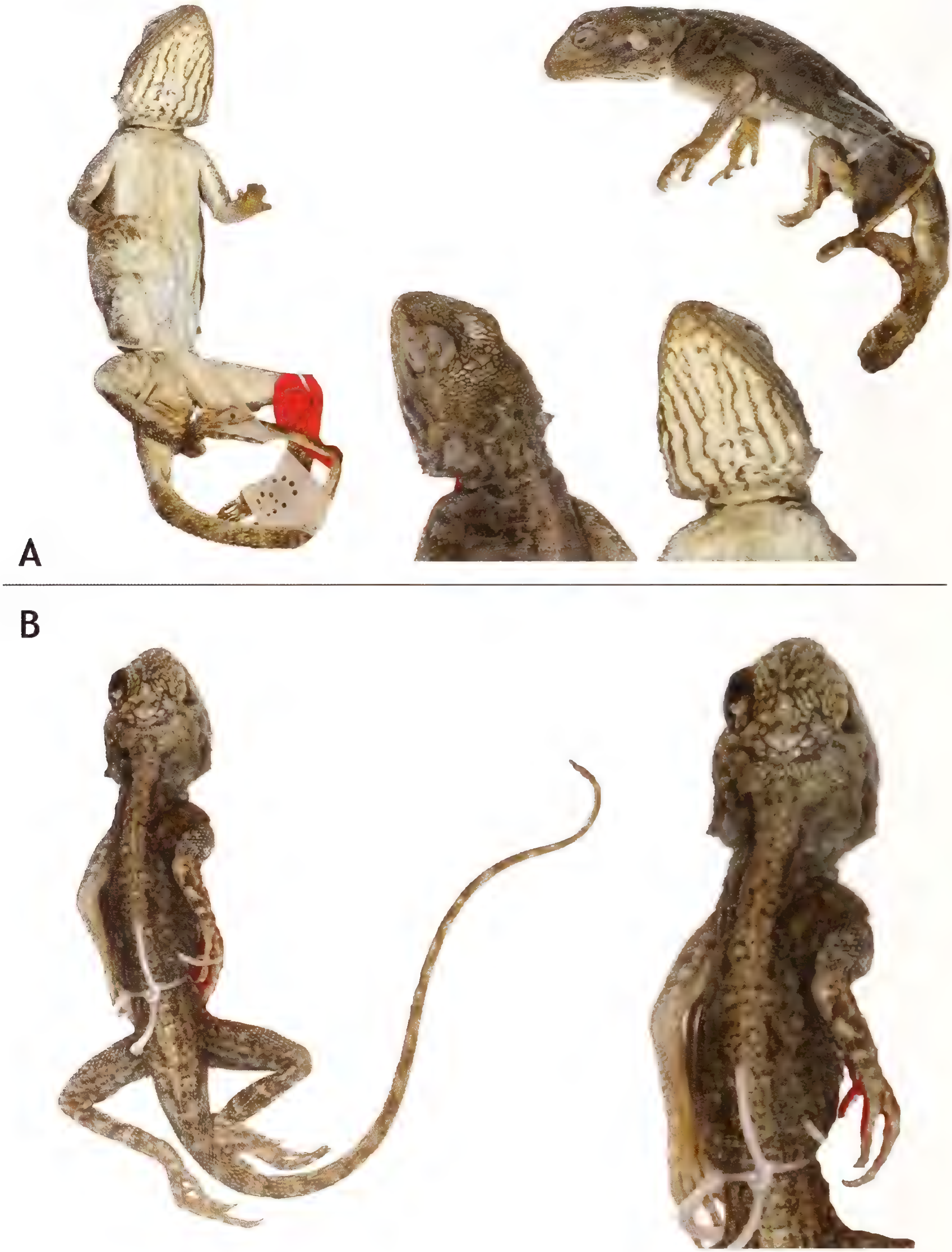

Fig. 1. The two syntypes of *Agama insularis* Chabanaud, 1918 (MNHN 1918.041-042).

Boulenger, 1884 from southern Africa and stated both as closely related. The only morphological differences noted were related to (1) head shapes (more elongate in *A. insularis*) and (2) body scalation (*A. insularis* has smaller scales, 120–130 scale rows around midbody versus about 90 in *A. kirkii*, and *A. insularis* had dorsal scales that are smaller compared to ventral scales.

Based on a larger series of specimens collected from the type locality, which included adult specimens, PARKER (1939) reassessed the validity of *A. insularis* (material of the IRSNB, Appendix 1). In this publication PARKER (1939) also compared *A. insularis* with *A. boulengeri* Lataste, 1886, a morphologically similar species distributed in Mauritania and Mali. He distinguished *A. insularis* from *A. boulengeri* by its more strongly carinate scales, especially on the occiput and lower surfaces of the tail; larger nasal, separated from the rostral by a single elongate scale; larger number of labial scales, 8–9 versus 11 and the colouration of adult males. Nevertheless, PARKER (1939) only described the adult colouration from preserved specimens. Adult males are brownish black above with light specking, especially on the vertebral region; lower surfaces of the head, chest and abdomen are blackish-grey; middle of the gular region is jet black. JOGER (1979) described the adult male colouration of living *A. boulengeri* as follows: (1) ground colour pale gray-brown with transverse rows of white spots; (2) throat dirty white with longitudinal stripes, parts of the head gray-blue; (3) tail gray-blue and (4) a characteristic half-moon shaped black bar on the anterior margin of the shoulder. LAMBERT & MULLIÉ (1998) refer, beside the tail crest of the males, to the nuptial colouration of females as the most striking difference between the sexes of *A. boulengeri*. They describe the males as drab with uniform purple-grey coloured scales dorsally, whereas the females have a brilliant yellow mid-dorsal band with three approximately bat-shaped transverse bands on a bright orange background.

LAURENT (1947) reported a series of *Agama insularis* from Iles Roumé and a neighboring island, Île Kassa, and mentioned that the characters given by PARKER (1939) were in agreement with his specimens. However, LAURENT (1947) described additional sources of morphological variation, including 10 to 13 precloacal pores, 8 to 10 supralabial and 7 to 10 infralabial scales. Because of differences in the number of scale rows around midbody (Île Roumé: 115 to 125; Île Kassa: 143 to 147) he suggested that the Île Kassa population deserved subspecific status.

The taxonomic status of *Agama insularis* has been changed since these early studies. GUIBÉ (1954) listed *A. insularis* as valid in the type catalogue of the collection of the Muséum national d'histoire naturelle in Paris, although WERMUTH (1967) regarded this species as questionable, since it was only known at this time from its type locality. JOGER (1979) reasserted the validity of *A. insularis*; however, MOODY (1980) placed *A. insularis* in synonymy of *A. boulengeri*, but without giving a reason. Nevertheless, BÖHME (1985) followed JOGER (1979) and stated that *A. insularis* and *A. boulengeri* are both valid species and probably closely related. Finally, BRYGOO (1988) and ULBER & BARTS (1997) treated *A. insularis* as a valid species, although without offering additional comments regarding this decision.

Interestingly, another species of *Agama* from West Africa possessing a prominent tail crest has remained mostly overlooked since its description. *Agama cristata* was described by MOCQUARD (1905) from a single specimen collected from Bomanesco (Sankaran) in Guinea by M. A. Chevalier, and later donated to the Muséum national d'histoire naturelle in Paris by M. Maurice de Rothschild. MOCQUARD (1905) did not compare his new species with any other species and characterized it mainly by the large crest proceeding from the neck to the tail. Later, *A. cristata* was apparently regarded as a synonym of *A. sankaranica* Chabanaud, 1918 by GUIBÉ (1954) and WERMUTH (1967), presumably because both taxa share the same type locality (*A. sankaranica*: Moussaia, Sankaran, Guinea; *A. cristata*: Bomanesco, Sankaran, Guinea). Later, BRYGOO (1988) confirmed the validity of *A. cristata* in his type catalogue presumably because of the tail crest, but again he was not followed by ULMER & BARTS (1997).

Despite the presence of a prominent tail crest in adult males shared between *Agama cristata, A. boulengeri* and the island endemic species, *Agama insularis,* a comparison of these species remains to be conducted. In contrast to the previous three species, *A. sankaranica* and *Agama weidholzi* Wettstein, 1932 are small and solitary-living species. The latter was included in the comparison, because it is endemic to this region and so far only known from Senegal (e.g. WETTSTEIN 1932), Gambia (BÖHME 2005), Mali (e.g. GRANDISON 1969) and Guinea-Bissau (MONARD 1940). Additionally, MONARD (1940) included specimens of *A. weidholzi* and *A. sankaranica* in the type series of *A. boensis*. (GRANDISON 1969, BÖHME 2005) and for that reason a close relation to *A. sankaranica* could be possible.

Our aim is therefore to compare the species of *Agama* with prominent tail crests in adult males (*Agama cristata, A. boulengeri* and the island endemic species, *Agama insularis*) to clarify their taxonomic status, distribution, and phylogenetic relationships. We also include other species of West African *Agama* in our study that lack prominent tail crests in adult males, but that are hypothesized to be close relatives because they occur in the same areas.

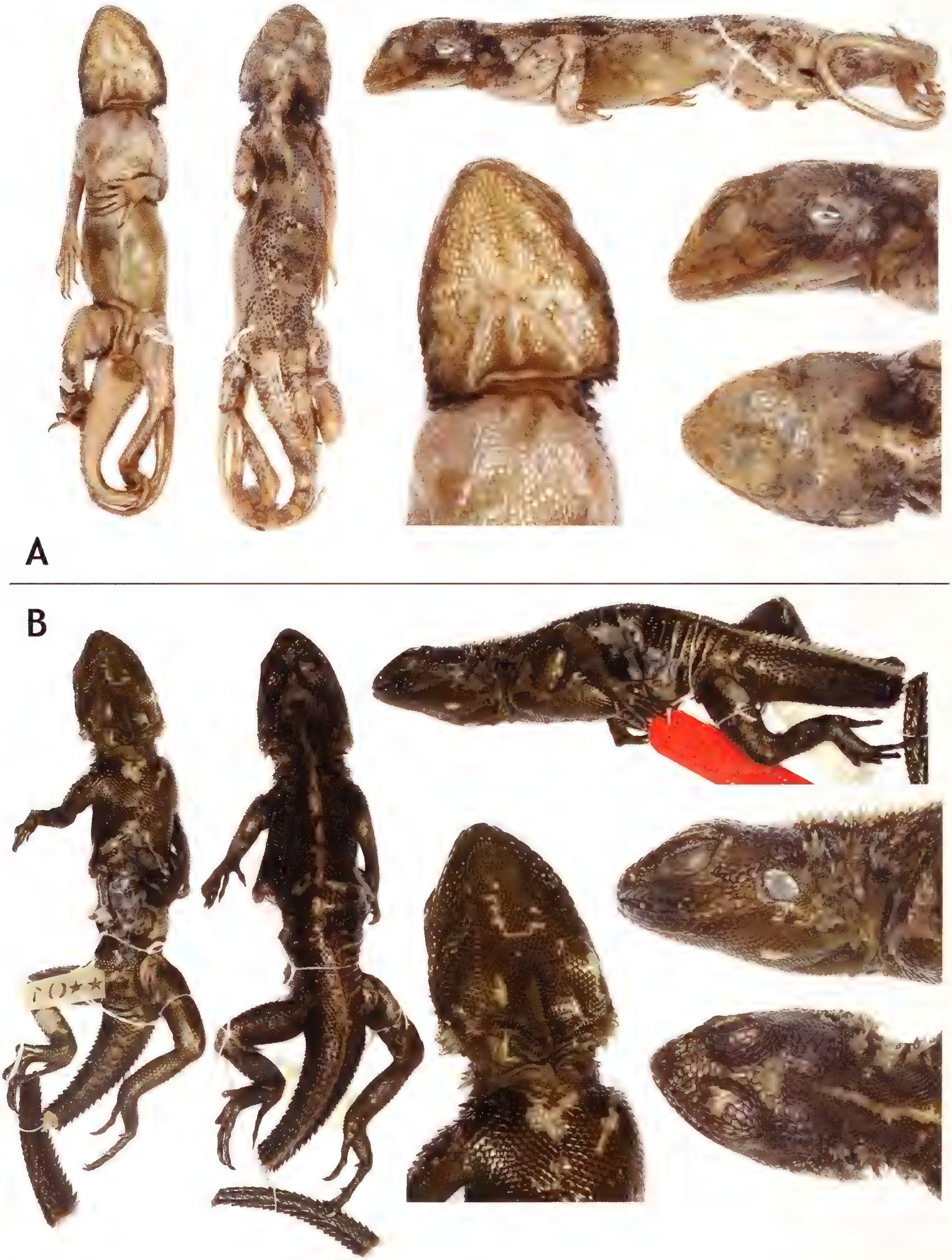

Fig. 2. The holotypes of a) *Agama sankaranica* (MNHN 1901.0395) and b) *Agama cristata* (MNHN 1901.0394).

MATERIAL & METHODS

The voucher specimens examined in this study are accessioned in the following natural history collections: Collection of Jean François Trape, deposited in Institut de Recherche pour le Développement (IRD) Dakar, Senegal (TR); Institut royal des Sciences naturelles de Belgique (IRSNB); Museum national d'histoire naturelle de Paris, France (MNHN; Museum für Naturkunde, Berlin, Germany (ZMB) and Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany. The type specimens of *Agama cristata* and *A. insularis* were included, however, the type specimens of *A. insularis* are juveniles and therefore topotypical material was also used for this taxon.

Since several studies have now shown that DNA barcoding, especially when using the mitochondrial 16S rRNA gene, is a reliable tool in reptile or amphibian taxonomy (e.g. VENCES et al. 2005; BWONG et al. 2009) molecular data were collected to calculate a simple neighbour-joining phylogeny (fig. 4) and to analyse the sequence variation between species. A portion of the mitochondrial 16S rRNA gene of *Agama insularis* (ZFMK 88247; GenBank accession number: GU133326) from the type locality, as well as *Agama cristata* (TR555; GenBank accession number: GU133325) from Guinea, *Agama boulengeri* (MNHN; Gen-Bank accession number: GU133324) from Mauritania, *Agama weidholzi* (ZFMK 75001; GenBank accession number: GU133328) from Gambia, *Agama sankaranica* (ZFMK 84992; GenBank accession number: GU133327) from an unknown locality and *Agama agama* (ZFMK 15222 [neotype]; GenBank accession number: GU133323) were sequenced. *Acanthocercus atricollis* (ZFMK 41748; GenBank accession number: GU133322) was used as outgroup.

DNA was extracted using QuiAmp tissue extraction kits (Quiagen) or a modified Chelex-Protocol (WALSH et al. 1991, SCHMITZ 2003). The primers 16sar-L (light chain; 5' – CGC CTG TTT ATC AAA AAC AT – 3') and 16sbr-H (heavy chain; 5' – CCG GTC TGA ACT CAG ATC ACG T – 3') of PALUMBI et al. (1991) were used to amplify a portion of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure was as described in SCHMITZ et al. (2005). PCR products were purified using Quiaquick purification kits (Quiagen). Sequences were obtained using an automatic sequencer (ABI 377). Sequences were aligned using ClustalX (THOMPSON et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (HALL 1999). A preliminary phylogenetic tree was calculated in the program Paup* 4.0b10 (SWOFFORD 2002) using the Neighbor-joining algorithm (NJ) and 20000 pseudo-replicates to estimate node support. This program was also used to compute the uncorrected pairwise distances for all sequences.

The following measurements and scale counts were used to compare the different species in statistical analysis (for selected characters see table 1): Snout-vent length (SVL): measured from mental scale to cloaca; tail length (TL): measured from cloaca to tip of tail; Tail crest length (TcL): length of the tail crest from midpoint of pelvic region to tip of crest; head length (HL): measured from jugale to rostral scale; head height (HH): measured at the jugal-postorbital region; head width (HW): measured across the jugal-postorbital region just anterior to the external auditory meatus; Midbody scales (MS): scale rows around midbody; tail crest scales (TcS): number of tail crest scales, counted from midpoint of pelvic region to tip of crest; dorsal scales (DS): number of midline longitudinal dorsal scales, counted from midpoint of pectoral region to midpoint of pelvic region; cloacal pores (CP).

Excel 2000 and SPSS (10.0) software packages were used to run statistical analyses. Hierarchical Cluster analysis and Principal Component Analysis (PCA) were used to evaluate the morphological data and to explore the phenetic relationships between the taxa examined.

RESULTS & DISUSSION

Morphology. Significant differences were found when the effect of body sizes was removed from analyses (see fig. 3), but there is still a high level of overlap among species in all PC's. Best results were found in PC 1 and 2 (PC 1= 41.379% of variance; PC 2= 25.825% of variance; PC 3= 24.098% of variance; PC 4= 8.699% of variance) and are visualized in fig. 3. *Agama insularis* has a significantly larger relative head height, head width and head length than *A. boulengeri*, but lower average of mid-body scale rows and significantly smaller relative head length than *A. cristata*. *Agama cristata* differs significantly in a higher average of mid-body scale rows and larger relative head length from both *A. insularis* and *A. boulengeri*. *Agama boulengeri* differs significantly in smaller relative head height, head width and head length from both *A. insularis* and *A. cristata*. Males have significantly lower tail-crest-scales and tail-crest-length than either *A. insularis* or *A. cristata*. Differences in pholidosis between *A. boulengeri* and *A. cristata* are low and mostly overlapping (see table 1), which is unsurprising within the genus *Agama*. But in average, *A. cristata* has a higher count of scale rows around midbody than *A. boulengeri*. Also the differences in colouration between *A. boulengeri* and *A. cristata* are low. Small differences in colouration were found between *Agama boulengeri* on one hand and *A. cristata* on the other hand. Especially the colouration of the throat in adult

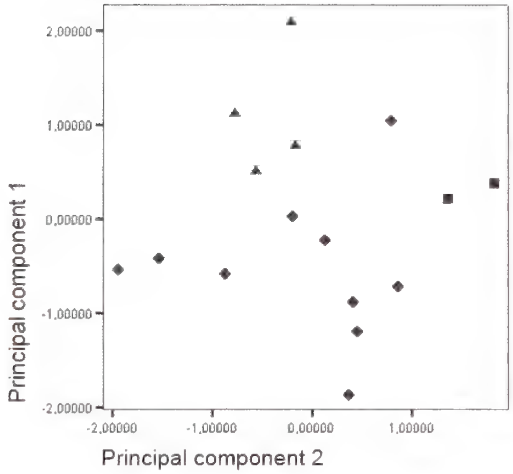

Fig. 3. Projection of the first and second principal component from a PCA run on 16 individuals assigned to ◆ = *Agama boulengeri*, ▲ = *Agama insularis* ■ = *Agama cristata*.

males is distinct. In *A. boulengeri* the throat is dirty white with longitudinal stripes, whereas in *A. cristata* the basal parts of the throat are dark bluish-black.

Genetics. As obvious from fig. 4, *Agama boulengeri* is very distinct from the two other known species with tail crests (*A. insularis*; *A. cristata*), and it is found in a basal position to all other *Agama* species included in this study (NJ: 70). In contrast, the two other species, *A. insularis* and *A. cristata* form a maximally supported clade (NJ: 100) that is the sister clade of *A. weidholzi* (NJ: 84) with this subclade significantly separated from its sister clade containing *A. agama* and *A. sankaranica* as sister taxa, though this latter subclade receives hardly any support (NJ: 56). This low support comes as no surprise as other studies show clearly that *A. agama* and *A. sankaranica* are not very closely related (Leaché et al. 2009).

Table 2 summarizes the uncorrected p-distances for 496 bp of the 16S rRNA gene. *Agama boulengeri* shows the highest genetic differences to all other species with values ranging from 12.1%–15.9% thus showing that it is not closely related to any of the other included *Agama* species, and is far removed from the two other taxa with tail crests (*A. insularis*: 15.5% *A. cristata*: 14.1%). Thus the genetic data clearly confirm the specific distinctness of *A. cristata*/*A. insularis* from *A. boulengeri*.

Although genetic interspecific differences range at moderately high values ranging from 8.0%–11.9%, the genetic distance between *A. insularis* and *A. cristata* is low at only ca. 0.7% (corresponding to only differing basepairs). The low level of sequence divergence observed between *A. cristata* and *A. insularis* is consistent with the hypothesis that these taxa represent a single species.

Agama boulengeri is distinct in pholidosis, colouration and genetics from *A. insularis* and *A. cristata*. But no significant differences in morphology and genetics were found between *A. cristata* and *A. insularis*. It is important to note that this result is based on an examination of type specimens, topotypical material, and freshly collected material (see appendix). Therefore we consider *Agama insularis* Chabanaud, 1918 as a junior synonym of the revalidated *Agama cristata* Mocquard, 1905.

Agama cristata Mocquard, 1905

1905 *Agama cristata* Mocquard, Bull. Mus. Hist. Nat. 11: 288.
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1997 *Agama insularis* – Ulber & Barts, Herprint International, Bredell, South Africa, 418 pp.
2008 *Agama maria* nom. nov. Barabanov, Russ. J. Herp. 15: 206.
2009 *Agama cristata* – Wagner & Böhme, Russ. J. Herp. 16: 161–162.

Holotype. MNHN 1901.0394.

Terra typica. Bomanesco, Sankaran, Guinea.

Comment on Nomenclature. Barabanov (2008) recently proposed a nomen novum for *Agama cristata* Mocquard, 1905 because he recognized this taxon as a primary junior homonym of *Agama cristata* Merrem, 1820, recently known as the iguanid lizard *Corytophanes cristatus*. However, Wagner & Böhme (2009) did not accept this suggestion because in accordance to article 23.9.5 of the ICZN (1999) the author failed to refer the case to the Com-

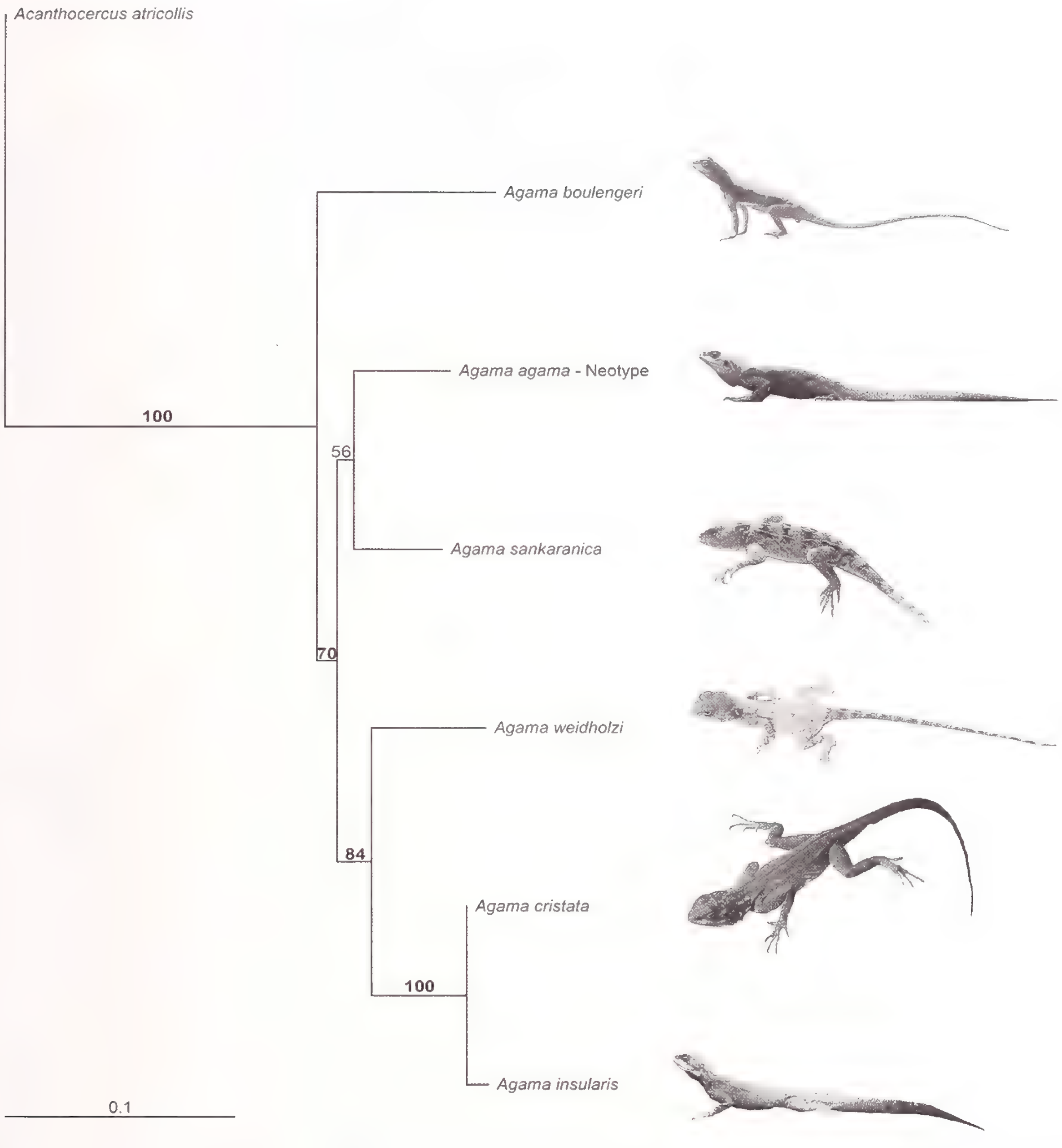
Acanthocercus atricollis
Agama boulengeri
Agama agama - Neotype
100
56
Agama sankaranica
70
Agama weidholzi
84
Agama cristata
100
Agama insularis
0.1

Fig. 4. Neighbor-joining tree based on 496 bp of the mitochondrial 16S rRNA gene. Values above the nodes represent bootstrap (20000 pseudo-replicates) values in percent for the neighbor-joining analysis. Significantly supported values are in bold. Values below 50% are not shown.

mission of Zoological Nomenclature which would be necessary because both taxa are not congeneric since 1827, where Boie (in Schlegel 1827) connects Merrem's *cristata* as type species with his newly described genus *Corythophanes*.

Diagnosis. A large species of *Agama* (total length of adult male up to 340 mm), which is characterized by its bluish-black colouration on the throat and the large nuchal and tail crests of adult males.

The species differs from nearly all other *Agama* species in having a large tail crest, usually reaching the last third of the tail. Only three other species, *A. boulengeri*, *A. kirkii* and *A. knobeli*, have such a prominent tail crest.

Agama cristata differs in detail from:

(1) *A. boulengeri* in (a) higher numbers of scales rows around midbody (97 to 123 in *A. boulengeri* and 111 to 147 [latter value fide Laurent 1947] in *A. cristata*); in

Table 1. Comparison of measurements and pholidosis.

	Agama boulengeri average (min–max), n	*Agama cristata* average (min–max), n	*Agama weidholzi**	*Agama gracilimembris**
SVL	**88.4** (62.5–129.8), 22	**92.0** (69.0–123.0), 16	54–65	44–57
TL	**185.0** (119.2–236.2), 12	**149.3** (98.8–215.0), 12	–	–
HH	**11.0** (8.1–16.3), 22	**12.3** (8.6–17.6), 16	–	–
HW	**16.1** (12.0–24.0), 22	**17.5** (11.1–23.8), 16	–	–
HL	**23.8** (17.0–33.6), 22	**25.3** (20.1–33.3), 16	–	–
SAM	**112.9** (97–123), 22	**121.4** (111–136), 13	68–82	70–85
TCS	**71.3** (62–78), 10	**77.5** (75–80), 6	–	–
PP	**11.3** (8–14), 12	**11.4** (10–13), 7	–	–

SVL= snout-vent length; **TL**= tail length; **HH**= head height; **HW**= head width; **HL**= head length; **SAM**= scale rows around midbody; **TCS**= tail crest scales; **PP**= precloacal pores. All measurements in mm;.*= after Grandison 1969

Table 2. Uncorrected p-distances for 496 bp of the mitochondrial 16SrRNA sequences used in this study.

	Taxa	**1**	**2**	**3**	**4**	**5**	**6**	**7**
1	*Acanthocercus atricollis* ZFMK 41748	–						
2	*Agama boulengeri* MNHN	0.2135	–					
3	*Agama agama* ZFMK 15222	0.2029	0.1348	–				
4	*Agama cristata* TR555	0.1937	0.1405	0.1040	–			
5	*Agama insularis* ZFMK 88247	0.2022	0.1553	0.1123	0.0072	–		
6	*Agama sankaranica* ZFMK 84992	0.1929	0.1209	0.0803	0.1036	0.1192	–	
7	*Agama weidholzi* ZFMK 75001	0.2117	0.1590	0.1069	0.0892	0.1002	0.1068	–

(b) having smaller relative head height, head width and head length; and (c) males of *A. boulengeri* have a lower number of tail-crest-scales and a lower length of the tail-crest. (d) male coloration (larger ocelli, lower parts of the throat and gular fold deep bluish-black).

(2) *A. kirkii* in (a) having smaller body scales; (b) dorsal scales are smaller than ventral scales; and (c) in having no narrow blue and white banded tail (d) a geographic distribution confined to northern parts of southern Africa (Malawi, Zambia, Zimbabwe, Mozambique, Botswana).

(3) *A. knobeli* is herein recognized as a valid species, because we recognized striking dissimilarities in morphology between *A. knobeli* and the former nominate form *A. atra*: *Agama atra* is lacking the prominent large tail crest and has more spinose scales as *A. knobeli*, but further research on the relationships of these two species is in need. However, *A. knobeli* differs from *A. cristata* in (a) having larger body scales, (b) dorsal scales in same size as ventral scales and (c) in having a pale vertebral stripe in nuptial coloured adult males, and (d) a geographic distribution restricted to Namibia.

Colouration in alcohol. The holotype of *A. cristata* is uniform brown. Syntypes of *A. insularis* are grey to brown in different shades, but typical ocelli of *Agama* females and juveniles are visible. One subadult female specimen (TR 2353) from the island Île de Roumé (Los islands) is uniform brown with scattered orange stripes and bars on the body and shows dark stripes on a white throat. Even juveniles from the same locality show dark framed ocelli on the body and white dots on the head. In both juveniles (MNHN 2008.0023, TR 2352) a lateral orange stripe is obvious.

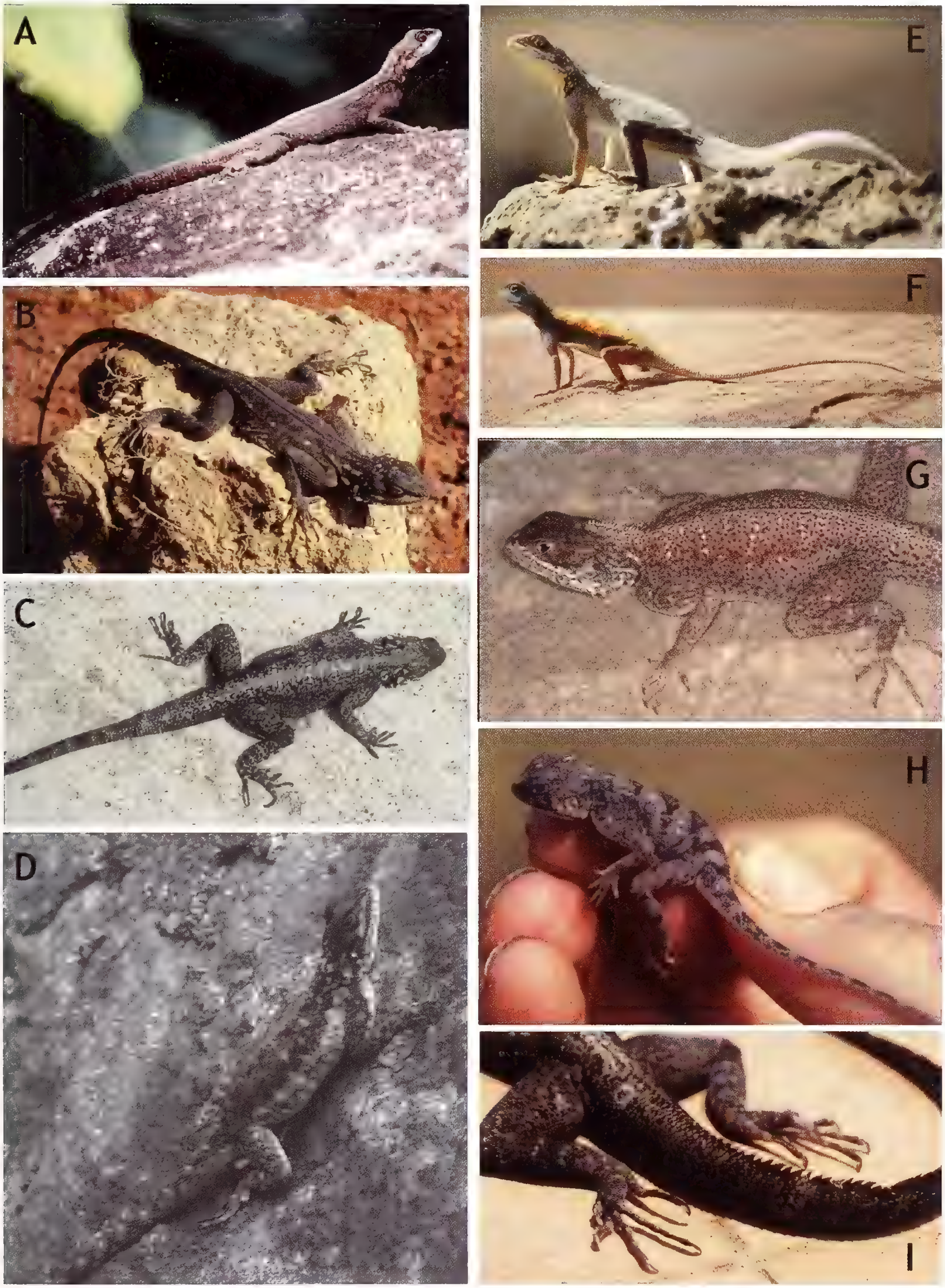

Fig. 5. Images of the following *Agama* species (in life):
A= '*Agama insularis*' from island Roumé (photo by Dr. Guy Kremer). **B**= *Agama cristata*, male, from Kindia, Pastoria, Guinea (photo by Ivan Ineich). **C**= *Agama cristata*, male, from Chutes de Kinkon, Guinea (photo by Ivan Ineich). **D**= *Agama cristata*, female, from Chutes de Kinkon, Guinea (photo by Ivan Ineich). **E**= *Agama boulengeri*, male, from Mauritania (photo by Hemmo Nickel). **F**= *Agama boulengeri*, female, from Mauritania (photo by Hemmo Nickel). **G**= *Agama boulengeri*, male, from Chûtes de Félou, Mali (photo by Ulrich Joger). **H**= *Agama weidholzi*, male, from Mali (photo by Ulrich Joger). **I**= *Agama cristata*, male, from Kindia, Pastoria, Guinea (tail crest in detail) (photo by Ivan Ineich).

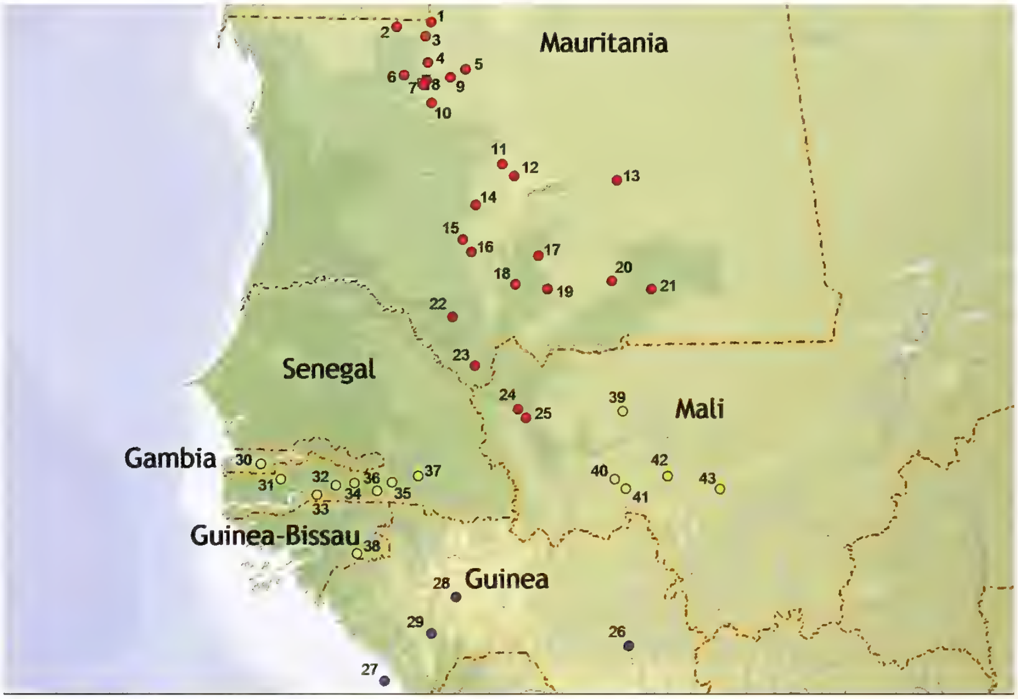

Fig. 6. Distribution map of *Agama boulengeri*, *A. cristata* and *A. weidholzi*.
Agama boulengeri: Mauritania: **1**= Choûm; **2**= Ben Amira; **3**= Aggui; **4**= Guelta Molomhar; **5**= Chinguetti; **6**= Guelta Hamdoun; **7**= Kanoal; **8**= Terjît; **9**= Zerga Mountains; **10**= Tintâne; **11**= Iriji; **12**= Tidjikja; **13**= Tîchît; **14**= Guelta Fanar; **14**= Guelta Matmata; **15**= Achram; **16**= Aïn El Ghaire; **17**= Bou Bleïine; **18**= Kîfa; **19**= Bougari; **19a**= Guelta Oumm Lebare; **19b**= Guelta Metraucha; **19c**= Oumm El Khez; **20**= Ayoûn El Atroûs; **21**= between Timbedgha and Ayoûn El Atroûs; **22**= Mbout; **23**= Sélibabi (for details see Padial 2006). Mali: **24**= Medine (type locality of *A. boulengeri*); **25**= Chûtes du Félou (Joger 1981).
Agama cristata: Guinea: **26**= Moussaia, Sankaran (type locality of *A. cristata*); **27**= Île Rooma, Îles de Los (type locality of *A. insularis*); **28**= Chutes de Kinkon near Pita; **29**= Kindia. *Agama weidholzi:* The Gambia: **30**= Bwiam. Senegal: **31**= Boughari, Casamance; **32**= between Tiara and Mantiankani; **33**= 13 km Southwest of Kolda; **34**= Tabadienke, 30 km South of Diallakoto; **35**= 20 km S of Médina Gounas; **36**= 12 km West of Kounkané; **37**= 5 km East of Darsalam (Niokolo-Koba National Park). Guinea-Bissau: **38**= Madina do Boé, Pitche. Mali: **39**= 9 km North of Fatao (14°24'N, 9°29'W); **40**= 20 km West of Kita (13°03'N, 9°42'W); **41**= 5 km East of Kita (13°03'N, 9°25'W); **42**= between Négala and Kassaro (12°55'N, 8°40'W); **43**= Négala (12°52'N, 8°27'W)

Colouration in life (see fig. 5). *Males*. Body brownish, scattered with dark framed white to creamy ocelli, usually bigger ocelli form distinct rows. Lips creamy to bluish-creamy. Head and neck brownish with a pale stripe underneath the eye. Lower parts of the throat and gular fold deep bluish-black with strips running to the chin. Posterior part of the neck, body, parts of the hindlimb and tail sometimes speckled with white and dark scales. Sometimes a pale vertebral band between the limbs is obvious. Tail at the base pale speckled black, downwards brownish. Belly and underside of the limbs creamish to dark grey.

Females. Body brownish, scattered with dark framed white to creamy ocelli, when pregnant with dark orange to red coloured bands on the lateral body sides between the limbs. Sometimes lateral parts of the body white followed by a darker band and pale brownish on vertebral parts. Head and neck brownish with pale to yellow dots on the upper head and a pale stripe underneath the eye. Lips creamy to white.

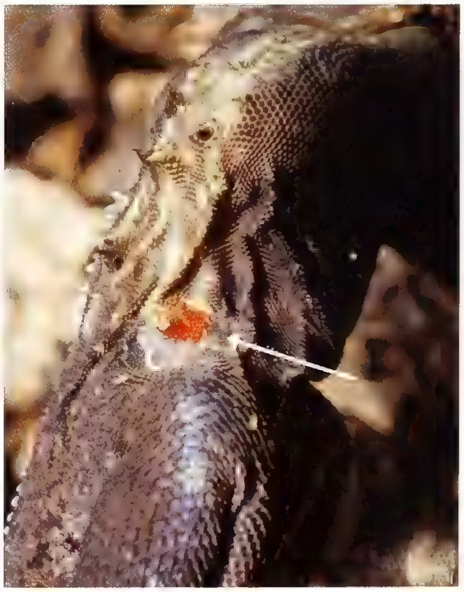

Fig. 7. Mite pocket-like structure (indicated by an arrow) at a specimen of *Agama cristata* from Kindia, Pastoria in Guinea.

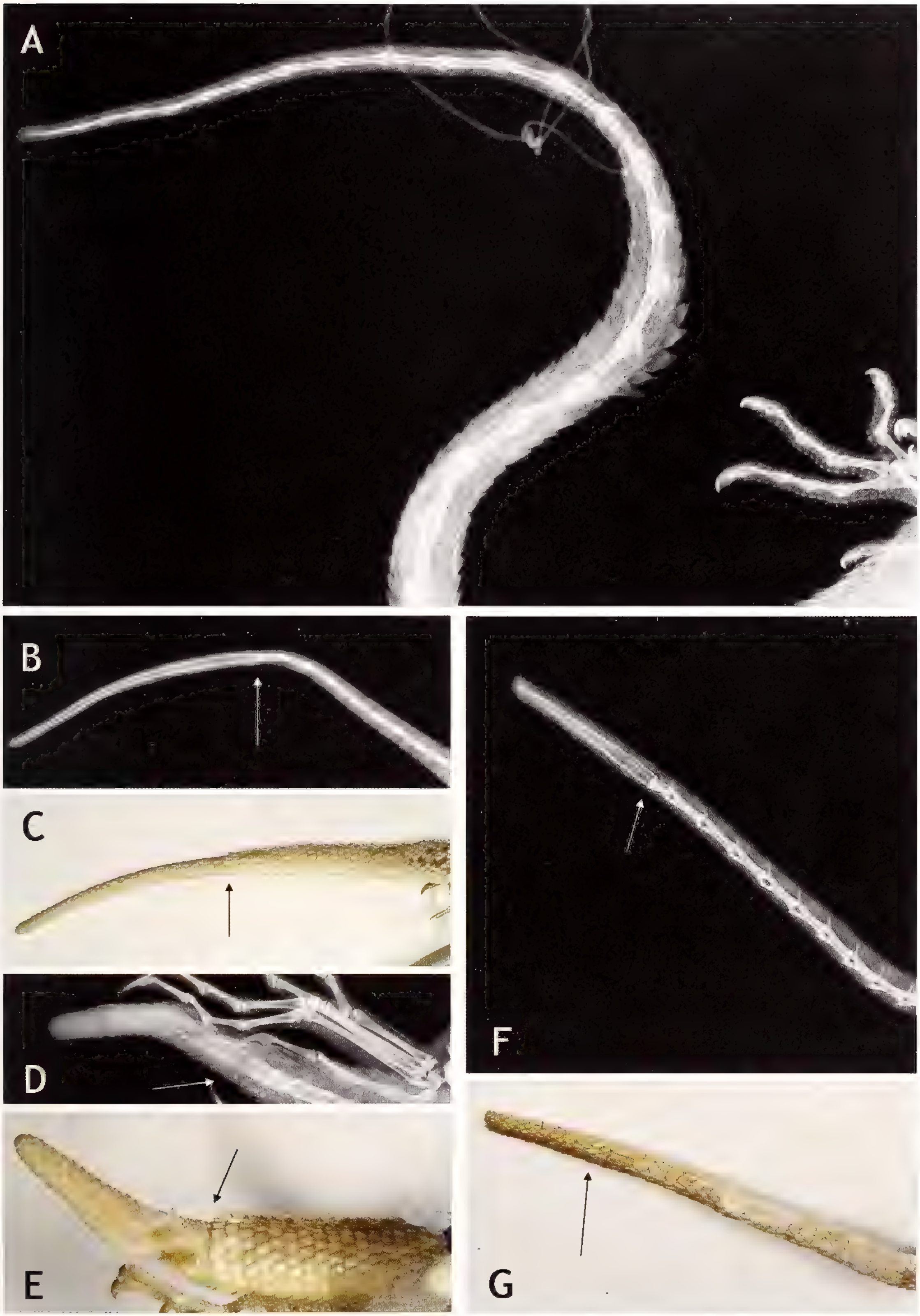

Fig. 8. Comparison of tail regenerates with x ray images (point of fracture indicated by arrows): **A)** original tail of *Agama boulengeri* (ZMB 22922). **B, C)** long tail regenerate of *A. boulengeri* (ZMB 55884). **D, E)** short tail regenerate of *A. boulengeri* (ZMB 55885). **F, G)** short tail regenerate of *A. boulengeri* (ZMB 55887)

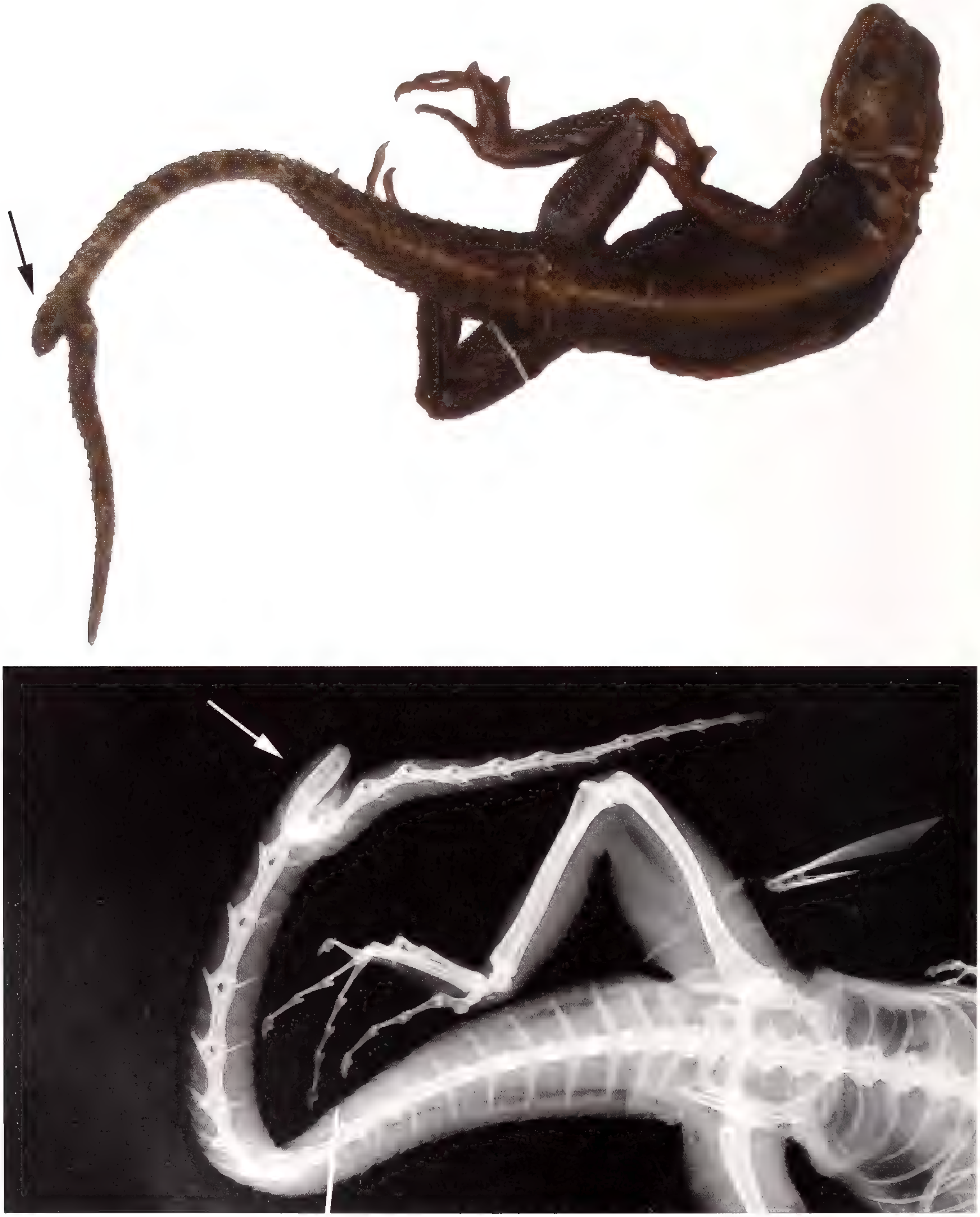

Fig. 9. A remarkable bifurcated tail in a specimen of *Agama lionotus lionotus* (Kenya: Kitui District, NMK L/1252).

Juveniles. Juveniles are only known from preserved vouchers.

Distribution. *A. cristata* is so far only known from Guinea. Beside the type localities of the two taxa, the species is also recorded from the hydroelectrical power station at Kinkon water falls (11°2'54.9"N 12°27'1.8"W; about 820 m a.s.l.) and the Pastoria station (former Institute Pasteur) (10°5'36.5"N 12°50'21"W; about 388 m a.s.l.).

Agama boulengeri is endemic to the oriental region from Senegal, western Mali and Mauritania (GENIEZ et al. 2004), which is a similar distribution pattern as in *Tarentola parvicarinata* JOGER, 1980 (Sauria: Phyllodactylidae) (Joger 1980). JOGER (1979) regarded the species as endemic for the Variscian Fold Mountains between the Adrar Mountains in Mauritania and northern Senegal (see fig. 6). The limits of the geographic distribution of *Agama cristata* are less clear, and it is therefore more difficult to discuss their speciation and biogeography. However, the Senegal River, which separates *A. boulengeri* from *A. cristata* may have functioned to keep these lineages separated.

Relationships. Morphologically, *A. cristata* is very similar to *A. boulengeri*. But preliminary phylogenetic results indicate a sister taxa relation between *A. cristata* and *A. weidholzi*, with *A. boulengeri* placed as the sister taxon to all species analyzed (fig. 4). These results do not correlate with morphology, because *A. weidholzi* is a small, ground dwelling species without any tail crest, and is similar in morphology to the west and central African species *A. gracilimembris*. GRANDISON (1969) compared series of the two species and stated both as closely related. GARTSHORE (1985) also mentioned similarities in the colouration of gravid females between *A. gracilimembris*, *A. doriae* and *A. sankaranica*. There are also similarities between *A. weidholzi*, *A. gracilimembris* and *A. sankaranica* in behavioural aspects. All these are solitary species that lack social interactions outside of the breeding season (GARTSHORE 1985), and males occupy home ranges but do not defend territories.

Unfortunately, *A. gracilimembris* could not be included in the phylogenetic analysis because of a lack of fresh DNA samples of this rare species.

Biology. *Agama cristata,* like *A. boulengeri*, is a rupicolous species living on rocks in syntopy with *Trachylepis quinquetaeniata* (Sauria: Scincidae). Also *Trachylepis affinis* was recorded in the area nearby. In males, a mite pocket behind the tympanum is sometimes obvious (see fig. 7). These mite pocket-like structures are rare in agamid lizards. ARNOLD (1986) described nuchal pockets from iguanian lizards whereas BERTRAND & MODRY (2004) reported the first pocket-like structures in an *Agama* lizard (*Agama caudospinosa*). In this case, the newly described mite *Pterygosoma livingstonei* was found heavily concentrated in a skin-fold in front of the forelimb. Here, we report a similar pocket-like structure in front of the forelimb of an *Agama cristata* specimen (fig. 7, indicated by an arrow), which is similar to the pocket shown in BERTRAND & MODRY (2004). However, these species are not closely related, and we predict that these structures are more common in *Agama* lizards than they are currently believed to be.

Remarks on caudal anatomy. Some specimens of *Agama cristata* and *A. boulengeri* (e.g. a subadult female; TR 2353) show remarkable tail regeneration (fig. 8). Complete caudal regeneration in Agamid lizards is relatively rare, and regenerated tails are normally short and possess a knob-like end (e.g. *Agama lionotus*, see fig. 9). This is probably because Agamidae, like Chamaeleonidae and Platynota, lack a cartilaginous stratum or plane (ANANJEVA 1985, ANANJEVA & DANOV 1991). As an example, the total length of a specimen of *A. cristata* (TR 2352) is 89.5 mm; with a tail length (TL) in total of 68.8 mm and a regenerate length (RL) of 36.2 mm (RL/TL= 0.53). Therefore, the regenerate measures a bit more than half of the length of the tail. The total length of the regenerate is longer than the documented bifurcated tail of *Laudakia caucasia* (ANANJEVA & DANOV 1991) with a length of 23.1 mm.

This phenomenon is also visible in *A. boulengeri*. Three specimens of the ZMB collection show a relatively long, slender and not knobbly regenerated tail. ZMB 55885 has a TL of 45.8 mm with a RL of 19.7 mm (RL/TL= 0.43). ZMB 55887 has a TL of 75.2 mm with a RL of 16.8 mm (RL/TL= 0.22), whereas ZMB 55884 has a TL of 109.6 mm with a RL of 46.4 mm (RL/TL= 0.42) (see fig. 8).

Also a specimen of the species *Agama lionotus lionotus* Boulenger, 1896 from East Africa (Kenya: Kitui District, NMK L/1252) shows a remarkable bifurcated tail, but here, in difference to the bifurcated tail reported by ANANJEVA & DANOV (1991) from *Laudakia caucasia*, only one tail tip is a regenerate (see fig. 9).

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Appendix. Material examined

Agama boulengeri: Mali. Kayes: Chûtes de Félou (ZFMK 20058, 22176 – 180, 25481 – 485). Mauritania. Adrar: Terjit (ZFMK 76917); 20km N Atar (ZFMK 79729); Ayoun-el Atrons (ZFMK 83825 – 827); Guelta Metraucha (ZFMK 76862 – 864, 76868); Galoula (=Passe de Galoula) (ZMB 32583, ZMB 55882 – 888, ZMB 32584).

Agama cristata: Guinea. Chûtes Kinkon (MNHN 2006.0553, MNHN 2006.0554); Kindia, Institut Pasteur (MNHN 2006.0555, MNHN 2006.0556).

'Agama insularis': Guinea. Îles des Los, Île Roumé (MNHN 2008.0023, TR 2352 – 53; IRSNB 1392 a–c, 1728, 1733, 1729 a–e; MNHN 2008.0023, ZFMK 88247).

Agama weidholzi: Gambia. Bwiam (ZFMK 75001). Mali. 8km E Kassaro (ZFMK 20060); 5km E Kita (ZFMK 20061); 20km W Kita (ZFMK 20062); 9km N Fatao (ZFMK 20063 – 65); between Negala and Kassaro (ZFMK 20059). Senegal. 5km SO Darsalam (ZFMK 20066 – 068); 20km S Medina Gounas (ZFMK 20069); 13km SE Kolda (ZFMK 20066 – 078); 12km W Kounkané (ZFMK 20070 – 071); between Tiara and Mantiankani (ZFMK 20072).

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Remarks on the type specimen of *Gonocephalus mjobergi* Smith, 1925 (Sauria: Agamidae)

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Abstract. The type specimen of *Gonocephalus mjobergi* Smith, 1925 has been re-examined. A remarkable character, longitudinal folds in the gular region has been discovered which is unique among agamids of the genus *Gonocephalus* Kaup. *G. mjobergi* has been compared to members of the genera *Ptyctolaemus* and *Mantheyus* and it is concluded that these genera form a monophyletic group and *G. mjobergi* is referred to as "Gen. A." *mjobergi* until further material becomes available.

Keywords. Agamidae, *Gonocephalus mjobergi*, type specimen.

INTRODUCTION

Historically, the genus *Gonocephalus* Kaup, 1825 included at some stage species from the genera *Acanthosaura* Gray, 1831, *Coryphophylax* Blyth, 1860 and *Hypsilurus* Peters, 1867 (see for example Boulenger 1885, Smith 1935 and Wermuth 1967). Moody (1980) removed all species belonging to the Melanesian-Australian radiation and Andaman-Nicobar species from its synonymy with *Gonocephalus* Kaup and revived the genera *Coryphophylax* (Blyth) and *Hypsilurus* (Peters) as well as *Arua* (Doria). The *Hypsilurus* and *Arua* species complex has been reviewed in detail more recently by Manthey & Denzer (2006).

Most *Gonocephalus* species were reviewed by Manthey & Denzer in the early 1990ies and arranged in species groups (Manthey & Denzer 1991) on grounds of morphological similarities. There are currently five groups recognised:

a) *bornensis* group including *beyschlagi, liogaster, bornensis, belli*, (*denzeri*) and the Philippine species *semperi, interruptus* and *sophiae* assigned to this group here.
b) *chamaeleontinus* group comprising *chamaeleontinus, doriae* (2 subspecies, *G. d. doriae* and *G. d. abbotti*) and *kuhlii*.
c) *megalepis* group comprising *megalepis, klossi, lacunosus*.
d) *robinsonii* group comprising *robinsonii* and *mjobergi* (tentatively assigned to this group by Manthey & Denzer 1991).
e) *grandis* group comprisiung only *grandis*.

Overall there are currently 17 species recognised with *G. denzeri* pending further material and verification. Manthey & Grossmann (1997) synonymised *G. denzeri* with *G. bornensis* because *G. bornensis* reveals a high variability in morphometric characters and pholidodis which includes characters of *G. denzeri*. The examination of additional 55 specimen and images of about 30 living specimen (Manthey unpubl.) including the type specimens of both species (RMNH 3043, 3044 and ZFMK 50527, 50528) gives rise to the assumption that *G. bornensis* and *G. denzeri* are conspecific. We note, however, that if just the type specimens are considered there are significant differences in dorsolateral pholidosis. While in *G. bornensis* dorsolateral scalation is homogeneous *G. denzeri* clearly shows clusters of enlarged scales dorsolaterally. Future phylogenetic studies using biomolecular and genetic methods will hopefully resolve this issue.

Morphologically the genus *Gonocephalus* is highly diverse and solely defined by a few characters, i. e. basal scales adjacent to the nuchal and dorsal crests, a transverse gular fold, a sharp canthus rostralis and an "angled" supra-

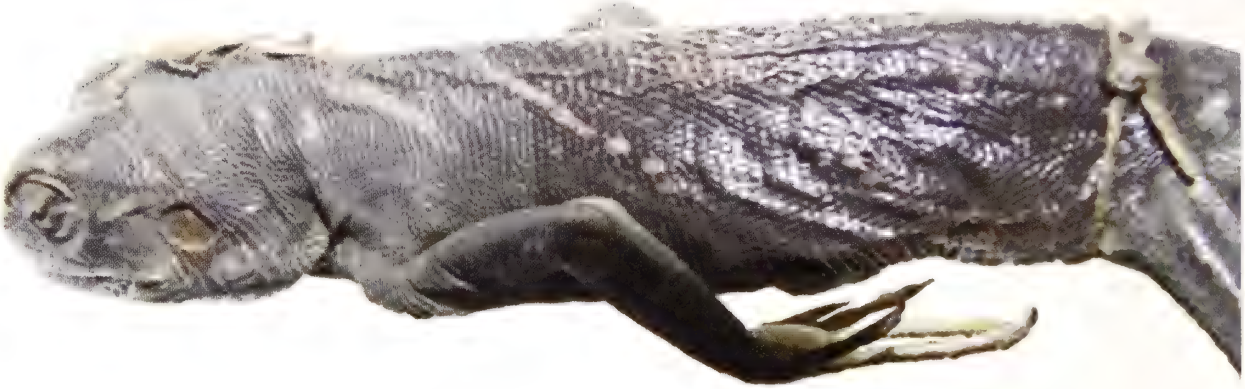

Fig. 1. Dorsolateral view of the type specimen (BMNH 1946.8.13.87) showing the oblique rows of enlarged dorsolateral scales.

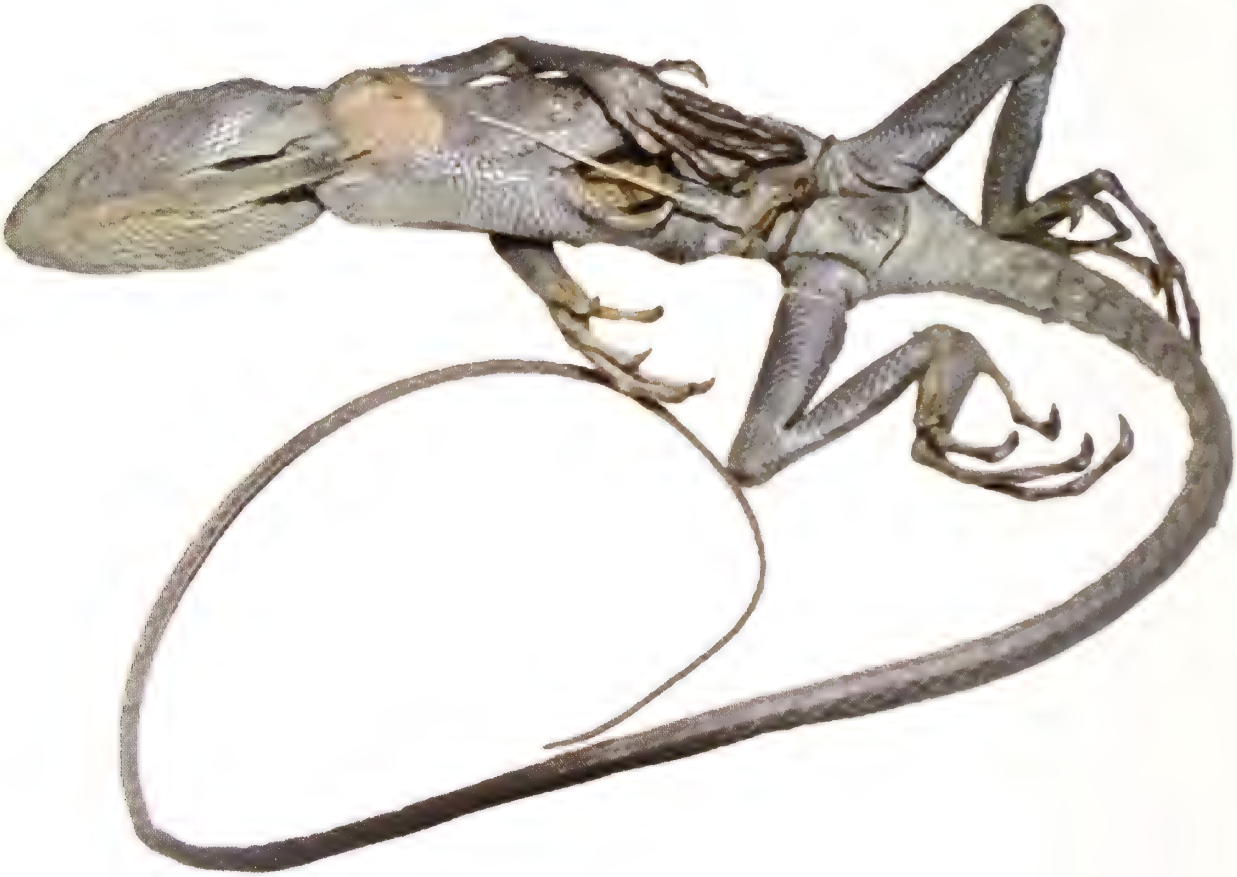

Fig. 2. Ventral view of the type specimen (BMNH 1946.8.13.87); note the clearly discernible longitudinal folds on the gular region.

ciliary ridge. Some of these characters are not well developed in several of the species groups above. The most resemblance to these generic features is exhibited by members of the *G. chamaeleontinus* species group.

Several species such as *G. grandis* and *G. robinsonii* show hardly any resemblance to the remaining species of the genus. An isolated species was described by SMITH (1925) as *Gonocephalus mjobergi* based on a single female specimen collected by Mjöberg on Mt. Murud at an altitude of 7000 feet (2134 m). Until today this has remained the only known adult specimen of the species. Owing to its superficial resemblance and shared ecological niche *G. robinsonii* and *G. mjobergi* were tentatively grouped by MANTHEY & DENZER (1991). In the course of our investigations into high altitude forms of *Gonocephalus* in particular *G. robinsonii* (Boulenger, 1908) we re-examined the type specimen of *G. mjobergi* (Smith, 1925).

RESULTS

Gonocephalus mjobergi was described on the basis of a single female collected on Mount Murud, Sarawak. Several features of type specimen are in poor condition. We re-examined the holotype (BMNH 1946.8.13.87, formerly BMNH 1924.8.28.8) and discovered characteristics not mentioned in the original description. While the gular sac is incomplete (SMITH l. c.: "the tip missing") it is difficult to determine its actual size. From the original drawings it could already be concluded that it might reach further onto the chest than in any other species of *Gonocephalus* except perhaps *G. robinsonii*. When we examined the holotype we were surprised that despite the incompleteness it was clear that the onset of a complete the gular sac would have reached the clavicular region. A feature clearly distinguishing *G. mjobergi* from all other *Gonocephalus* is the possession of enlarged dorsolateral scales forming oblique rows. The first row is located in the shoulder region and two distinct rows across the back as can be seen in Fig. 1. Dorsolaterally enlarged scales are present in some species of *Gonocephalus* from Sumatra, in particular *G. megalepis* (Bleeker, 1860), *G. klossi* Boulenger, 1920 and *G. lacunosus* Manthey & Denzer, 1991 but never in such a geometrical arrangement as can be found in the type specimen of *G. mjobergi*. Another feature in *G. mjobergi* is the possession of an enlarged platelike scale below the tympanum which is separated from the tympanum by two rows of small scales. Additionally, we discovered that *G. mjobergi* possesses two parallel longitudinal gular folds a feature not mentioned at all by Smith (l.c.). No other *Gonocephalus* species possesses this outstanding character which can clearly be seen in figure 2. Both folds start on the distal part of the gular region approximately bordering the serrated edge in the middle line of the pouch. The outer one runs nearly parallel to the centre line of the gular pouch and continues onto the anterior part of the chest. It partially conceals the *Gonocephalus* typical transverse fold. The inner folds are shorter and curve inside towards the centre line. This feature is very similar to the longitudinal gular folds known from species of the genera *Ptyctolaemus* Peters, 1864 and *Mantheyus* Ananjeva & Stuart, 2001. ANANJEVA & STUART (2001) depict the gular region of the latter two genera. The arrangement and colouration in *G. mjobergi* is rather comparable to that in *Ptyctolaemus*. It consists of two rows (grayish white in alcohol) with dark colouration of the skin in between. This indicates that this character independently developed in *Ptyctolaemus*, *Mantheyus* and *Gonocephalus mjobergi* and seems to be an autapomorphy. All three species also lack a transverse gular fold present in *Gonocephalus*.

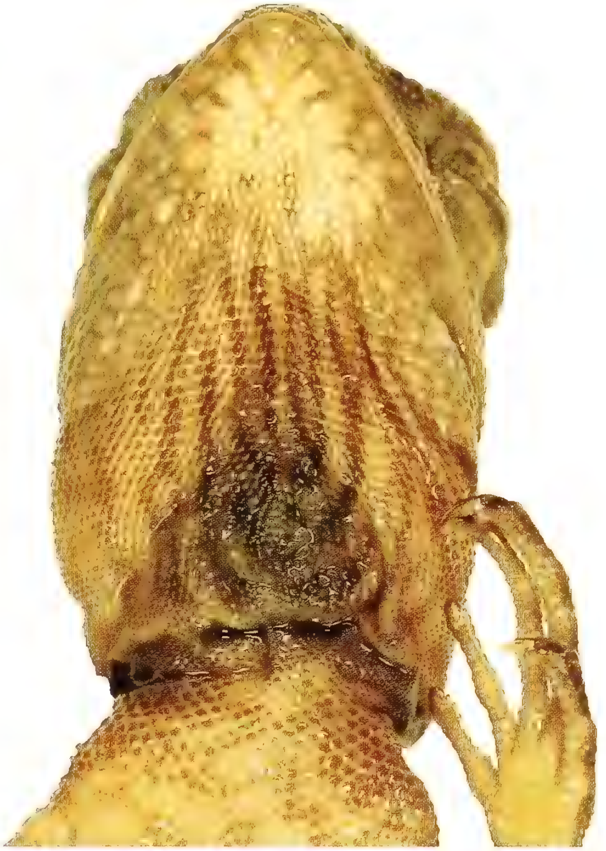
Fig. 3. Ventral view of the juvenile *Gonocephalus* sp. collected on Mt. Murud (ZRC 2.5953).

However, *G. mjobergi* is by no means congeneric with either *Ptyctolaemus* or *Mantheyus*. Both genera *Ptyctolaemus* and *Mantheyus* have scaled tympani as opposed to *G. mjobergi*; additionally, *Mantheyus* has femoral pores. Within this cluster only *G. mjobergi* shows oblique rows of enlarged dorsolateral scales. Because of the type specimen of *G. mjobergi* being a female we hypothesize that the gular sac will be even larger in male specimens which would distinguish it further from the genera discussed here with the exception of *G. robinsonii*.

As a consequence we propose to combine *Ptyctolaemus*, *Mantheyus* and *G. mjobergi* in a genus group with longitudinal gular folds being an autapomorph character for the cluster constituting a synapomorphy for the three genera, hence pointing towards monophyly of this group.

Owing to the lack of specimens for *G. mjobergi* we prefer to take a conservative view and not define a new monotypic genus until more material becomes available. Here we suggest to refer this species as "Genus A." *mjobergi.*

I. Das (University of Malaya) collected a specimen of a juvenile *Gonocephalus* on Mt. Murud and referred to it as *G. mjobergi*. This specimen has been depicted in Das (2006: 84) and was deposited in the Singapore Zoological Reference Collection (ZRC 2.5953). The colouration in life is a vivid green with darker reticulate pattern. This is in accordance with Smith's (l. c.) description of the colouration of the female which has been described as „grass-green in life". However, several other species of *Gonocephalus* show this kind of colouration. In particular juvenile specimens of *G. liogaster* (Günther, 1872) and *G. bornensis* (Schlegel, 1848) show a large resemblance to the specimen depicted by Das (l.c.) as can be seen for example in fig. 136 of Manthey & Grossmann (1997) and fig. 254 of Malkmus et al. (2002).

Additionally, the juvenile specimen from Mt. Murud does not possess enlarged dorsolateral scales or an enlarged scale below the tympanum as described for the type. Such a feature is, however, not depending on age and should be developed early on in life. A ventral view including details of the gular region is shown in figure 3. As can be seen the gular region of the juvenile specimen does not show any feature resembling parallel longitudinal folds and therefore propose that ZRC 2.5953 should be referred to as *Gonocephalus* sp. until more material for comparison becomes available.

Acknowledgements. We would like to thank Dr. Colin McCarthy (Natural History Museum London) who allowed us to examine the type specimen of *G. mjobergi* and Kelvin Lim (Zoological Reference Collection, Singapore) who provided photographs of the juvenile specimen deposited in his collection.

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Activity profiles, habitat selection and seasonality of body weight in a population of Arabian Spiny-tailed Lizards (*Uromastyx aegyptia microlepis* Blanford, 1875; Sauria: Agamidae) in Saudi Arabia

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Abstract. A field study was carried out on the Arabian Spiny-tailed Lizard (*Uromastyx aegyptia microlepis*) in Saudi Arabia (Mahazat as-Sayd Protected Area) focusing on seasonal differences in activity, body condition and on parameters influencing selection of burrow sites in this large desert-dwelling lizard. *Uromastyx a. microlepis* is highly seasonal in respect to activity/visibility outside of its burrows which provide shelter against unfavorable climatic conditions. At Mahazat as-Sayd these lizards exhibit a bimodal activity in spring and summer while activity in autumn is unimodal with a peak at early afternoon, but the overall activity is generally low at this time of the year. More than 73 % of total observed yearly activity takes place in spring and early summer. Seasonal changes in availability of food result in differences of the animals' body condition, with a significant decrease of body-mass between spring / autumn and summer / autumn respectively. Selection of burrow sites is largely influenced by soil type and vegetation coverage.

Key Words. Reptilia; Sauria; Agamidae; *Uromastyx*; *Uromastyx aegyptia microlepis*; seasonality; habitat selection; activity; body condition; Mahazat as-Sayd Protected Area; Saudi Arabia.

INTRODUCTION

The spiny-tailed lizards of the genus *Uromastyx* are inhabitants of the deserts and semi-deserts of North Africa, Arabia and the Middle East. Currently 15 species are considered to be valid, of which 6 are known to occur on the Arabian Peninsula (WILMS et al. 2009). There is a considerable scientific interest regarding the taxonomy and phylogeny of these animals but ecological knowledge remains scarce and fragmentary with most studies focusing on *Uromastyx nigriventris* and *Uromastyx aegyptia* (GRENOT & LOIRAT 1973; GRENOT 1976; BOUSKILA 1986; VERNET et al. 1988; CUNNINGHAM 2000, 2001; AL-HAZMI 2002; AL-JOHANY 2003; AL-HAZMI et al. 2005). This is especially interesting, considering the ecological importance, prevalence and local abundance of these animals.

Uromastyx aegyptia (Forsskål, 1775) is by far the largest member of the genus, reaching a maximum body length of even more than 700 mm and a weight up to 2.500 g (Fig. 1). Taxonomically, three subspecies, *Uromastyx a. aegyptia* (Forsskål, 1775), *Uromastyx a. microlepis* Blanford, 1875 and *Uromastyx a. leptieni* Wilms & Böhme, 2001 are distinguised (WILMS et al. 2009). The present study focuses on the Arabian Spiny-tailed Lizard (*U. a. microlepis*) which lives in deserts and semideserts of Arabia (Saudi Arabia, Yemen, Oman, United Arab Emirates, Qatar, Kuwait), in Jordan, Syria, Iraq and coastal Iran. Habitats show a marked seasonality regarding climatic parameters (temperature, air humidity, precipitation) as well as regarding availability of food. In contrast to the wide range of daily and annual fluctuations of air and soil temperatures, the temperatures within *Uromastyx* burrows are remarkably constant (WILMS & BÖHME 2007 & unpublished data). Therefore these burrows are considered to play an important role as refuges in respect to thermo- and hydroregulation and as shelter against predators. Burrows of *Uromastyx aegyptia* can be up to 1025 cm long and reach about 180 cm deep in the ground (BOUSKILA 1983, 1984), but are, at least at Mahazat as-Sayd, normally not longer than about 300–530 cm and 80–120 cm deep (own data).

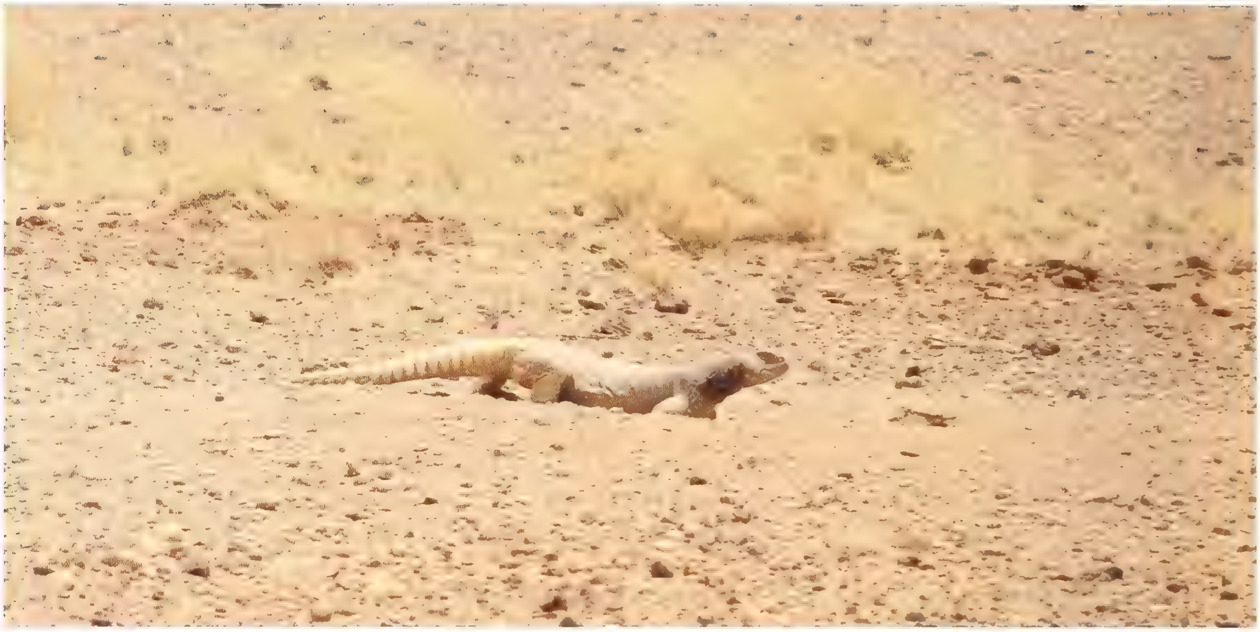

Fig. 1. Adult *Uromastyx aegyptia microlepis* at Mahazat as-Sayd, Saudi Arabia. Photo: T. WILMS.

The primary production of *Uromastyx* habitats is quite low and exhibits strong seasonal and annual differences. Therefore it is somewhat surprising that *Uromastyx aegyptia*, as all other species of the genus, is primarily herbivorous (MANDAVILLE 1965, KEVORK & AL-UTHMAN 1972, AL-OGILY & HUSSAIN 1983, BOUSKILA 1984 & 1987, ROBINSON 1995). Nevertheless remains of beetles (Tenebrionidae, Carabidae), ants, grasshoppers and even scorpions are also found in the stomach contents as well as in fecal pellets of all age classes (KEVORK & AL-UTHMAN 1972, WILMS 2007, pers. obs.). However, the proportion of animal matter in the food is very low and was estimated to be only about 1–2 % of total food intake.

The present paper analyzes the seasonality of activity and body condition in this species which is induced by the aforementioned environmental variability. A second focus was put on the selection of habitat structures by *Uromastyx a. microlepis*. This study was carried out on free ranging populations of *Uromastyx aegyptia microlepis* at Mahazat as-Sayd Protected Area, Saudi Arabia.

MATERIAL AND METHODS

Study Site

All fieldwork was carried out within the boundaries of Mahazat as-Sayd Protected Area, Saudi Arabia, which has been protected since 1989. Mahazat as-Sayd (22° 15' N, 41° 50' E) is located in central-western Saudi Arabia, approximately 170 kilometers north-east of Taif. The reserve is Saudi Arabia's only completely fenced wildlife reserve and is a reintroduction site for Houbara Bustards (*Chlamydotis undulata macqueenii*), Arabian Oryx (*Oryx leucoryx*) and Sand Gazelles (*Gazella subgutturosa*). Mahazat as-Sayd covers an area of 2244 km^2 and lies within one of the hottest regions of the world (MEIGS 1953). It is a hot and semi-arid to arid desert steppe habitat, typical of the central plateau of the Arabian Peninsula. The elevation is between 900–1050 m above sea level (LENAIN et al. 2004). The terrain of this area consisted of flat gravel plains, known as regs, occasionally interdigitated by dry sandy wadis (Fig. 2). Over 95 % of the area is covered by sand and gravel. Air temperature in Mahazat, as recorded in a standard weather shelter, often exceed 43 °C during the summer, and occasionally reaches 50 °C (SEDDON 1996, SHOBRAK 1996, WILLIAMS et al. 1999). Rainfall averages ca. 100 mm per year (WILLIAMS et al. 1999) and typically occurs between March and May each year, but with occasional important rain events at other times. There is no permanent source of water above ground level in Mahazat as-Sayd, but ephemeral pools exist for short periods after heavy rain (LENAIN et al. 2004).

The main study site was situated just south-east of the main gate to Mahazat as-Sayd (Al-Muwayh gate), covering an area of approx. 4 km^2 and was primarily used to assess habitat selection, while a second area nearby was chosen to establish a 60 km long transect for the evaluation of activity profiles.

The flat gravel plains in this part of the Arabian Desert are intersected by wadis and dominated by sparse vege-

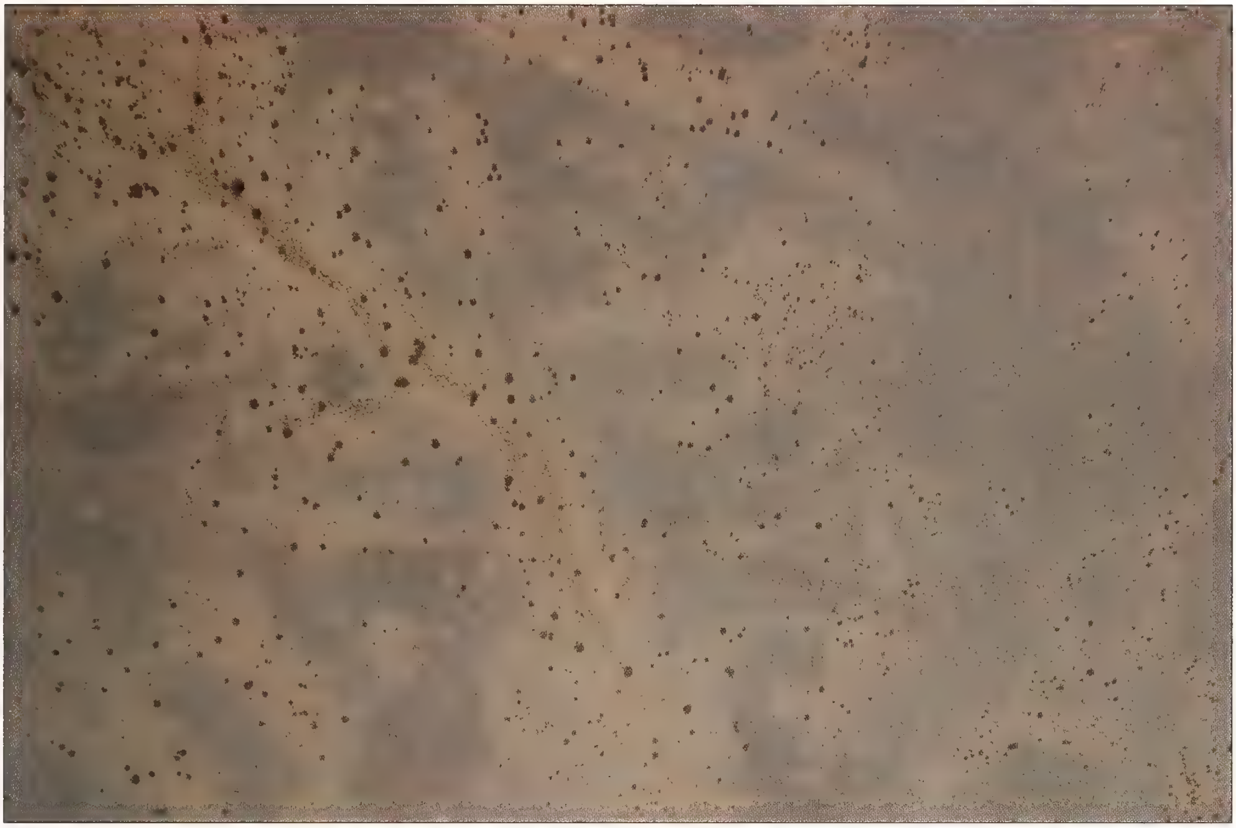

Fig. 2. Aerial view on the study site at Mahazat as-Sayd Protected Area showing reg formation with interdigitating sandy wadis. Photo: T. WILMS.

tation of perennial grasses, including *Stipagrostis* spec., *Panicum turgidum* and *Lasiurus scindicus*, and small trees, mainly *Acacia* spec. (MANDEVILLE 1990).

This study took place in spring, summer and autumn 2006 as well as spring and summer 2007.

Methods applied to assess activity profiles

To assess the differences in seasonal activity of the Spiny-tailed Lizards a transect was defined within an *Uromastyx* colony. The length of this transect was 60 km and it was driven with a 4 WD vehicle eight times per season (equals 480 km each) with an average speed of 40 km/h. These transects were driven only on sunny and calm days. As a result of this protocol the covered time per season was 12 hours (7 am–7 pm). The transect was driven in the following seasons: Summer 2006 (28th July–04th August), autumn 2006 (26th October–17th November), spring 2007 (30th March–06th April) and early summer 2007 (27th June–01st July).

The following data were registered by two persons (each concentrating on the area on either side of the transect): Presence of specimens (time), size class [juveniles (total length < 200 mm), subadults (total length 200–400 mm), adults (total length > 400 mm)], distance of specimen from respective burrow, animal behaviour (e.g. basking, shading, feeding), coloration (dark grey, bright yellow) and habitat (e.g. soil type, vegetation). To estimate the thermal environment of the observed specimens physical models were used to measure operative temperatures (T_e) in different microhabitats in summer 2006 and spring 2007 (HERTZ et al. 1993, SHINE & KEARNEY 2001). Hollow copper cylinders (230 mm long, 78 mm diameter, 0.6 mm wall thickness) were used as models. Miniature data loggers (i-buttons, Dallas Semiconductors, Model 1921) were placed in the model lumen to record T_e. Data loggers were calibrated in a water bath against a mercury-in-glass thermometer that had a calibration traceable to the National Institutes of Standards and Technology. To mimic the reflectance of a cold (grey colored) *Uromastyx* the model was covered with grey duct tape. Temperatures measured with the tape covered copper model followed the body temperatures of a dead *Uromastyx* better than temperatures measured with the uncovered model. Duct tape covered models were calibrated against dead as well as live *Uromastyx* under the original climate in the field (data will be published elsewhere).

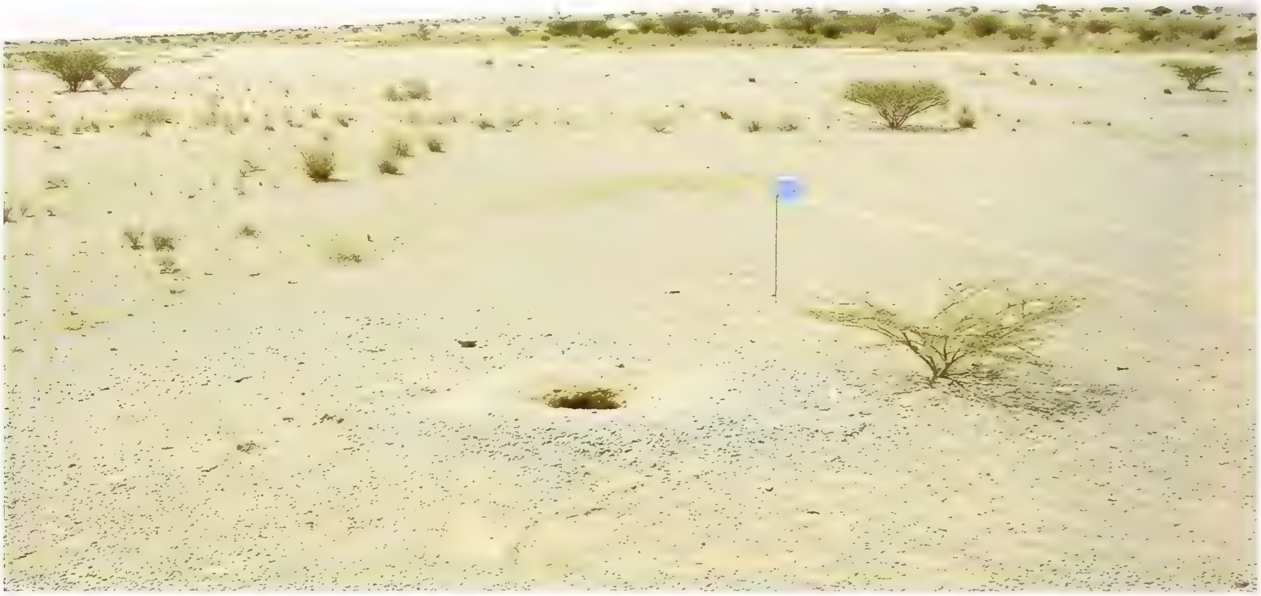

Fig. 3. *Uromastyx* burrow marked with a flag at the study site in Mahazat as-Sayd. Photo: T. WILMS.

Methods applied to assess habitat selection

The main study site was in spring 2006 systematically scanned for *Uromastyx* burrows by driving parallel transects (distances between transects ca. 50 meter). Each active burrow was marked with a flag (Fig. 3) and the following parameters were registered: Orientation of burrow entrance (N, NE, E, SE, S, SW, W, NW), soil type (fine sand, coarse sand, clay sand, sand/gravel mixture, fine gravel, medium gravel, coarse gravel, rock/sand mixture, rock), slope, vegetation coverage (0 %, < 5 %, < 15 %, < 25 %), distance to next *Acacia*. A total of 206 active *Uromastyx* burrows were registered. Burrows were considered as active (inhabited or visited) either if an *Uromastyx* was observed directly or if fresh tracks were found near the opened and clean burrow entrances. Otherwise, the burrow was classified as non-active (abandoned).

To assess habitat selection 80 burrows out of the 206 registered ones were selected randomly and tested against 80 additional random localities within the boundaries of the study site, for which the same parameters as for the active burrows were collected. $\chi 2$ analyses were performed to assess differences between burrow locations and randomly placed locations.

Methods applied to assess seasonality of body weight

At the main study site *Uromastyx* were trapped using snares put into the entrance of active burrows. Trapping was carried out in spring 2006 (08th May–2nd June), summer 2006 (15th July–01st August), autumn 2006 (20th October–11th November.) and spring 2007 (26th March–15th April). This trapping method has the advantage that a captured animal is still able to retreat into the burrow and therefore the risk of overheating and loosing the animal is minimized. Captured *Uromastyx* were marked with a passive integrated transponder (PIT), weighted, measured (total length, tail length, head length and width) and several scale counts were taken. Some specimens were implanted with temperature data loggers (i-buttons) and equipped with radio transmitters for a separate study on the thermobiology of *Uromastyx a. microlepis* (WILMS et al. in prep.). The specimens were subsequently released at their original burrow.

To assess seasonality of body condition, a body-mass-index (bmi) was calculated for each animal using the following quotient: *bmi = weight (g) / total length (cm)*. Only data of adult specimens (total length > 400 mm) were included in the analysis (n=62).

Statistical analyses of ecological data

The Excel 2000 and SPSS (15.0) statistical packages were used to run the analyses. $\chi 2$ analyses have been selected to evaluate activity data as well as data on habitat selection. To uncover differences in body-mass-indices Mann-Whitney *U*-test and Kruskal-Wallis statistical test were applied.

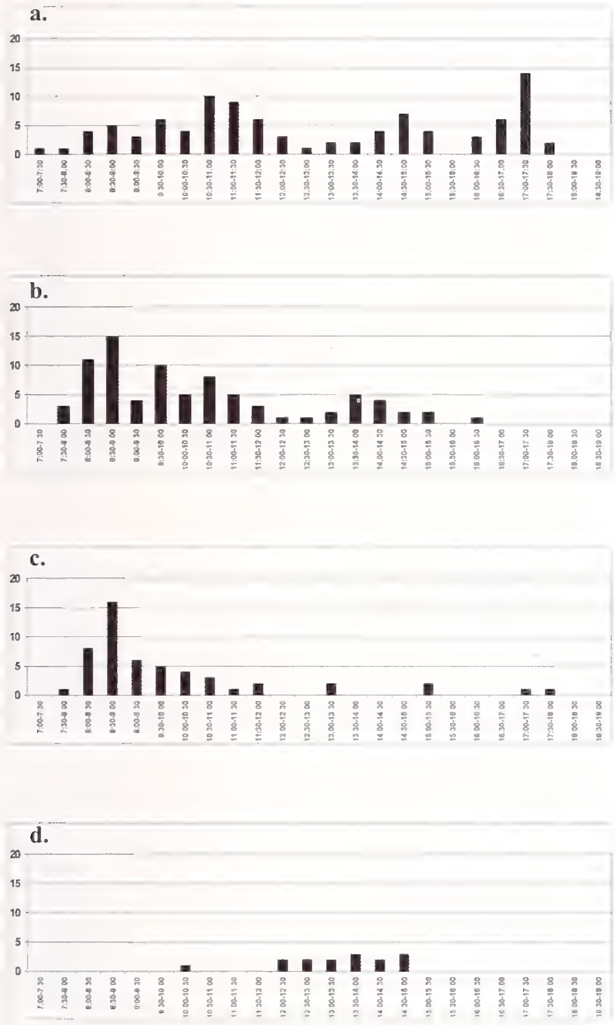

Fig. 4. Visibility profiles of *Uromastyx aegyptia microlepis* at Mahazat as-Sayd at different seasons; **a.** Spring; **b.** Early Summer; **c.** Summer; **d.** Autumn.

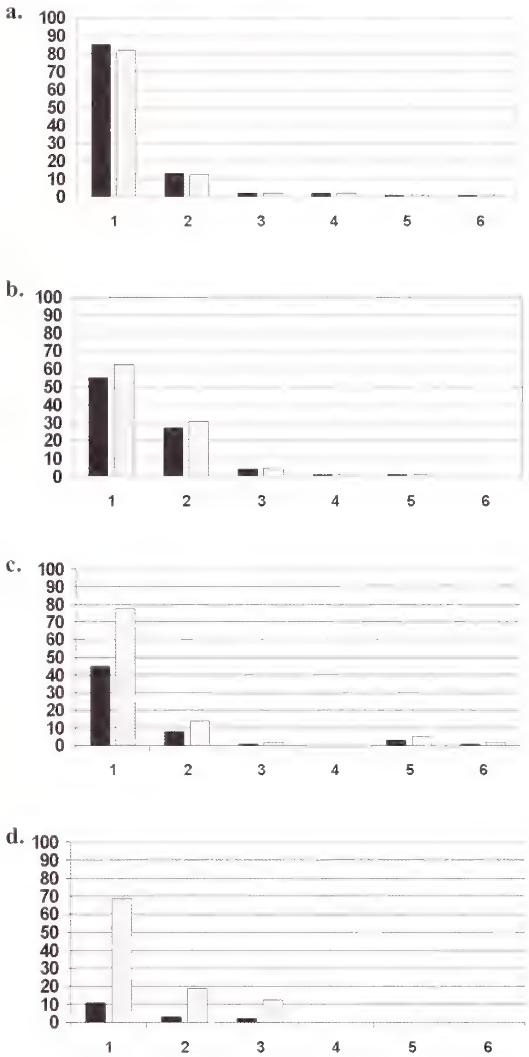

Fig. 5. Distribution of different behavioral activities as absolute numbers (black bars) and as percentage of total observations (grey bars) at different seasons; **a.** Spring; **b.** Early Summer; **c.** Summer; **d.** Autumn.
Behavior: **1.** Basking near burrow entrance; **2.** Animal far away from burrow entrance; **3.** Shading under *Acacia* tree; **4.** Feeding; **5.** Basking on a bush; **6.** Basking on a stone.

RESULTS

Activity structures

A total of 245 *Uromastyx* were sighted while driving the transects. The absolute numbers for the respective seasons are: 97 (spring), 82 (early summer), 52 (summer), 14 (autumn). This is equivalent to 39.59 % (spring), 33.46 % (early summer), 21.22 % (summer) and 5.71 % (autumn) of total observed presence above ground. There is a very restricted activity during winter (deduced from own data on body temperatures, data not shown; BOUSKILA 1986, AL-HAZMI et al. 2005). These observations show that *Uromastyx a. microlepis* is highly seasonal at Mahazat as-Sayd ($\chi_2 = 65.74$, $P < 0.01$, $df = 3$), with a maximum visibility from spring to early summer.

Profiles of daily visibility were produced for every season by adding up the specimens observed within respective intervals of 30 minutes (Fig. 4). The diagrams show, that *U. a. microlepis* exhibits a bimodal rhythm in spring and early summer with two relatively high visibility peaks in spring (at morning from 10:30–11:00 hrs respectively afternoon from 17:00–17:30 hrs) but only one pronounced peak in early summer (at morning from 8:30–9:00 hrs), followed by a greatly reduced but nevertheless clearly visible peak at early afternoon (13:30–14:00 hrs). The profiles for spring and early summer exhibit a period with a significantly reduced visibility during the hottest time of

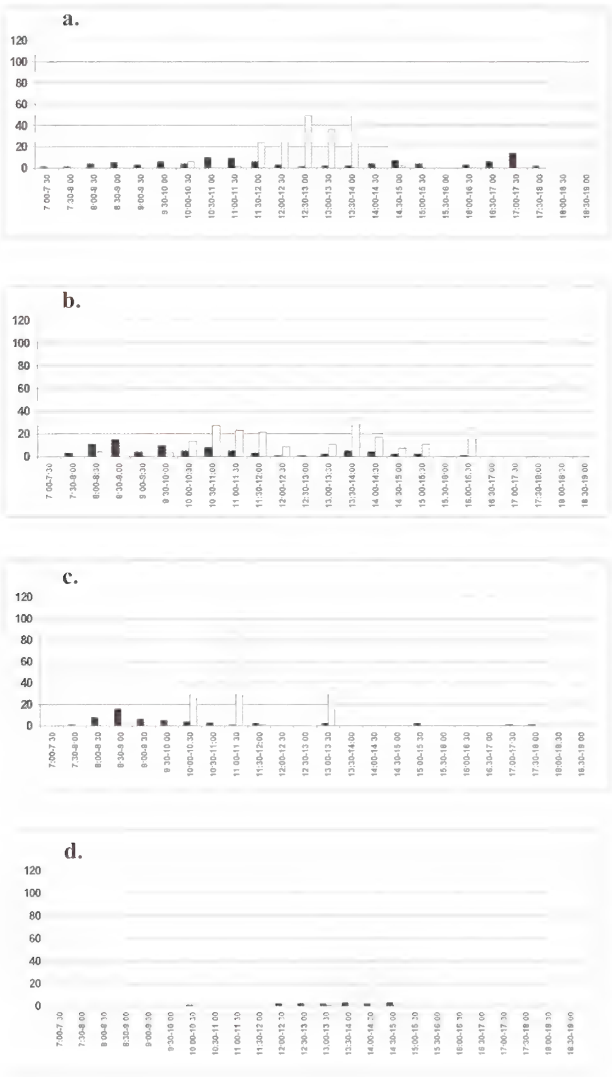

Fig. 6. Profiles showing the number of visible specimens (black bars) as well as average distances (in meters) of all observed specimens within each respective interval of 30 minutes (grey bars); **a.** Spring; **b.** Early Summer; **c.** Summer; **d.** Autumn.

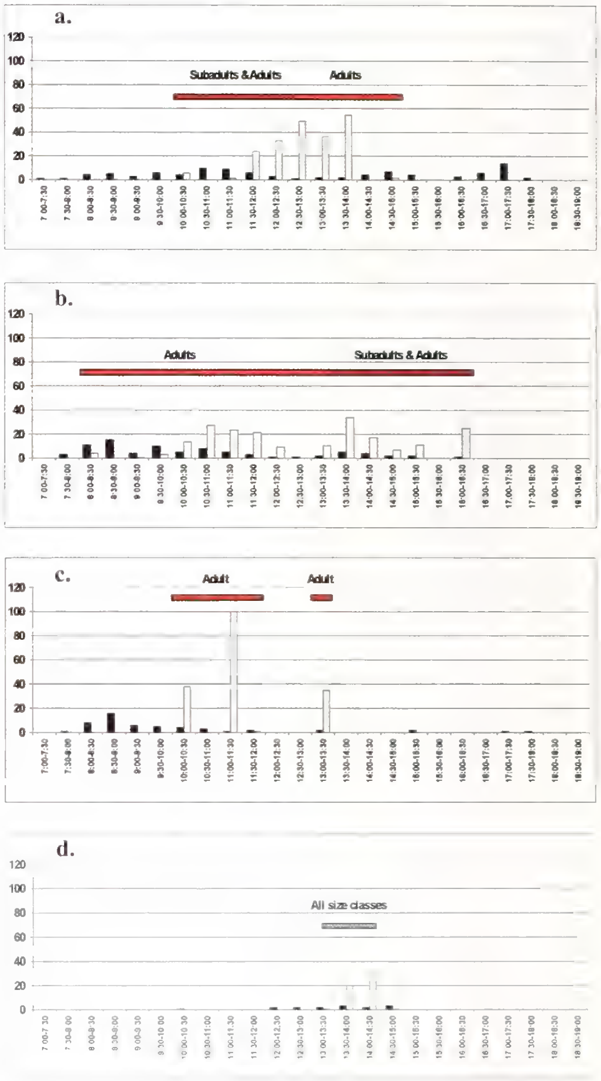

Fig. 7. Profiles showing the number of visible specimens (black bars) as well as the average distances (in meters) from the burrows (grey bars). Vertical bars indicate size class of active specimens. **a.** Spring; **b.** Early Summer; **c.** Summer; **d.** Autumn.

the day (12:30–14:00 hrs in spring; 12:00–13:30 hrs in early summer). The profile for the summer season shows principally also a bimodal visibility rhythm with the highest visibility between 8:30 hrs and 9:00 hrs followed by a rapid decrease of visibility. After 12:00 hrs specimens were seen only occasionally (two specimens between 13:00–13:30 hrs, three specimens between 15:00–15:30 hrs, one specimen at 17:26 hrs and one specimen at 17:34 hrs); but nevertheless some specimens were still visible. The comparison of the profiles from spring, early summer and summer show an obvious trend of reduction of afternoon visibility and a shift of the first visibility peak from late morning to early morning, which is possibly related to the increase of maximum day temperature. The visibility profile for autumn is unimodal and shows an overall very restricted level of visibility with a maximum occurring between 12:00 hrs and 15:00 hrs, then the warmest time of the day.

These visibility profiles were produced regardless of the type of observed activity, thus counting a visible specimen as being active. Figure 5 shows the distribution of the different activities like basking, shading, feeding and specimens being far outside of their respective burrow for all four observation periods as absolute numbers (black bars) as well as percentages thereof (grey bars). Calculation of χ_2 statistics showed that the observed seasonal differences are significant for the categories "basking near burrow entrance" ($\chi 2 = 57.451$, $P < 0.01$, df = 5) and "animal far outside of its burrow" ($\chi 2 = 24.000$, $P < 0.01$, df = 5), while differences in the other four categories were not significant. As a consequence, diagrams showing the number of visible animals as well as the average distance of specimens from their burrows during each 30 minute interval were created (Fig. 6).

Temperatures in spring are relatively mild, resulting in a prolonged time the lizards have to spend basking near the burrow entrance to reach their preferred body temperatures. After having reached the preferred body temperature some animals start leaving the direct vicinity of their own burrow. From 12:30–14:00 hrs presence of specimens is greatly reduced, but those animals still present exhibit a high degree of activity indicated by the long distance from their respective burrow (Fig. 6a). Evaluating the activity data in respect to animal size revealed, that from 12:07 hrs until 14:41 hrs only large adults were seen far outside of their burrows (Fig. 7a). Obviously temperatures during midday are even in spring high enough to force the juveniles and subadults under ground, seeking shelter in their burrows as thermal refuges and therefore accounts for the relatively low number of active specimens. In early summer average as well as absolute temperatures are higher than during spring, thus the basking period near the burrow entrance on early morning is shorter; thus resulting in an earlier start of "far from the burrow activity" (Fig. 6b). Obviously temperatures at morning are already too high to allow activity of juveniles and subadults away from their burrows because of the risk of overheating. From 8:28 hrs until 14:00 hrs only adults have been seen active. After 14:12 hrs also subadults started "far from the burrow activity" (Fig. 7b). In summer visibility of *Uromastyx* was generally greatly reduced. There was no observed activity of juveniles and subadults and only five adult specimens have been seen active during the period between 10:12–11:40 hrs and at 13:08 hrs and 13:25 hrs (Fig. 6c & 7c). In autumn visibility and activity is greatly reduced due to the low temperatures. Activity was observed for all size classes only during early afternoon (Fig. 6d & 7d).

Habitat selection

Of the five registered parameters at burrow locations three proved to show significant deviations between observed and expected frequencies. These are: orientation of burrow entrances ($P < 0.01$), soil type ($P < 0.01$), and vegetation coverage ($P < 0.01$). The slope of the area around burrow entrances as well as the distances of burrow entrances to next *Acacia* were not significantly different compared to circumstances at random locations (data not shown).

Orientation of burrow entrances: $\chi 2$ analysis revealed a significant deviation of the observed distribution of burrow entrance directions from the expected distribution of burrow entrance directions ($\chi 2 = 30.27$; $P < 0.01$; df =7). The highest deviation from the expected value exists for burrow entrances directed to south-west and south-east (Fig. 8).

Selected soil type at burrow location: Nine different soil types were found at the 80 randomly selected locations within the study area (fine sand, coarse sand, clay sand, sand/gravel mixture, fine gravel, medium gravel, coarse gravel, rock/sand mixture, rock). $\chi 2$ analysis of observed frequencies of selected soil types at burrow locations and of soil types at randomly placed locations within the study

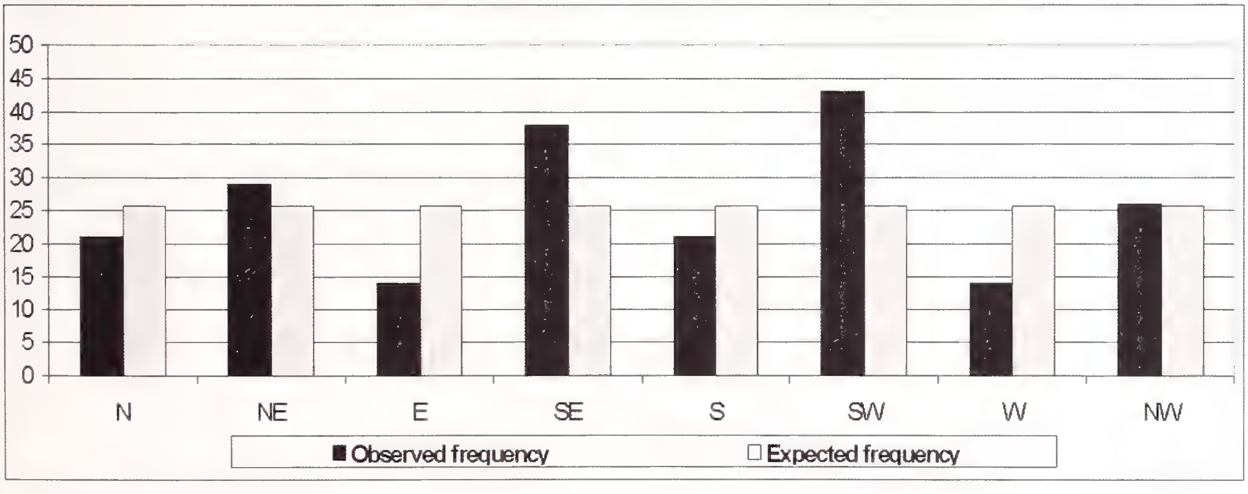

Fig. 8. Observed and expected frequencies of *Uromastyx* burrow entrance directions at Mahazat as-Sayd.

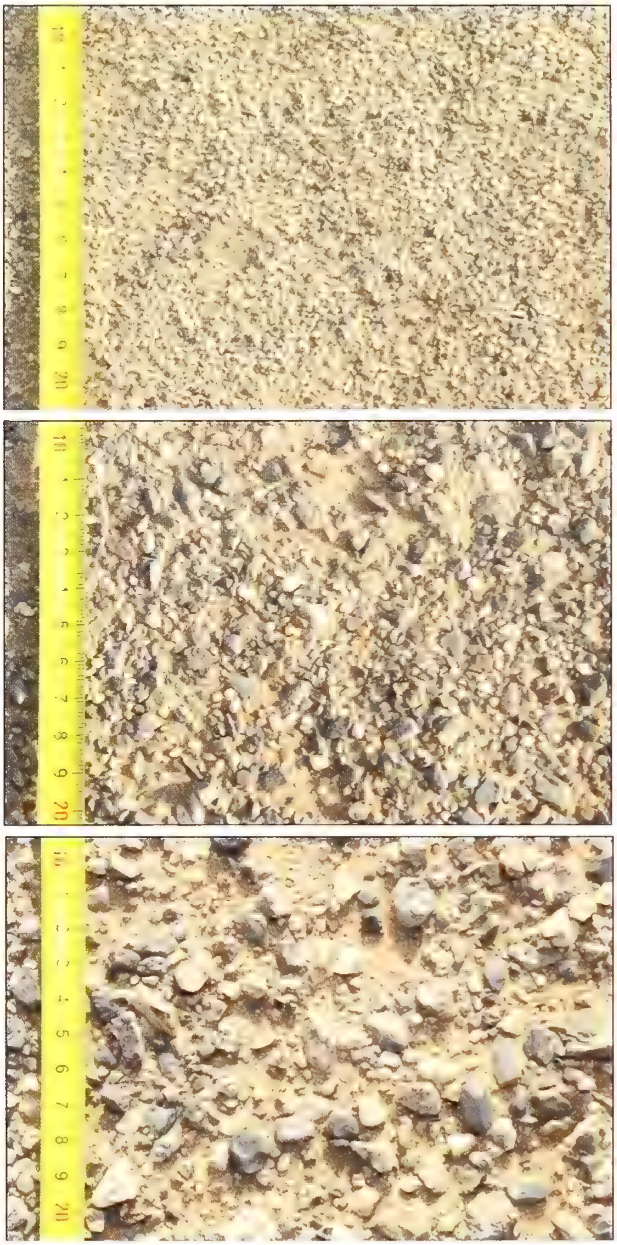

Fig. 9. Selected soil types at *Uromastyx* burrow locations **a.** coarse sand; **b.** fine gravel; **c.** medium gravel.

area revealed significant differences ($\chi_2 = 40.30$; $P < 0.01$; df = 8). All but one of the randomly selected *Uromastyx* burrows were located at places with medium gravel, fine gravel and coarse sand (Fig. 9). The only exceptional burrow was found between black rocks. Occasionally the original soil type in the vicinity of *Uromastyx* burrows was covered by a thin layer of drifting sand, which did not interfere with the physical properties of the under laying soil. In such cases only the main substrate was considered for the statistical analysis. Sandy soil was therefore defined as loose deep sand.

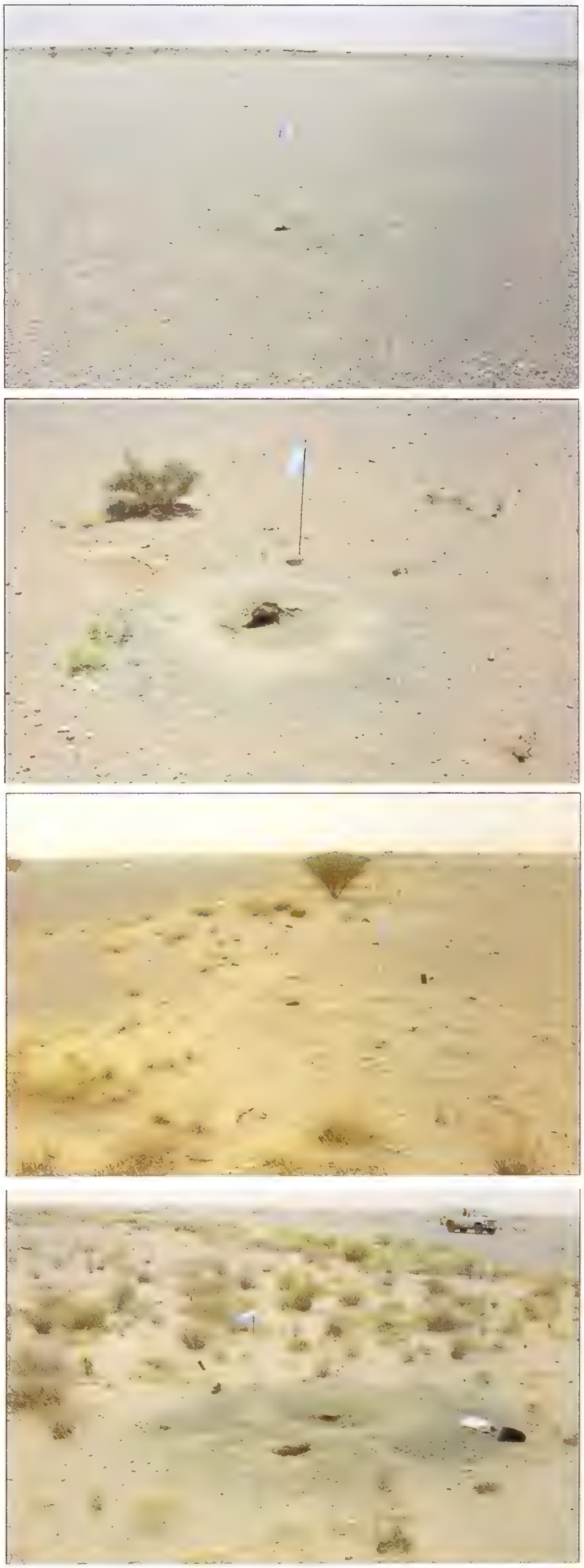

Fig. 10. Vegetation coverage estimated within a radius of five meters around entrances; **a.** 0 %; **b.** < 5 %; **c.** < 15 %; **d.** < 25 %.

Selected vegetation coverage at burrow location: Vegetation coverage was estimated within a radius of five meters around the burrow entrances respectively around the randomly selected locations (0 %, < 5 %, < 15 %, < 25 %; Fig. 10). χ_2 analysis revealed a significant difference between vegetation coverage frequency at burrow locations and at randomly placed locations ($\chi_2 = 49.40$; $P < 0.01$; $df = 3$). The data show that *Uromastyx* avoid area with 0 % coverage but show a preference for areas with < 5 % vegetation coverage. For places with < 15 % and < 25 % vegetation coverage no differences between observed and expected frequencies were evident.

Seasonality of body weight

Morphometric data of 62 adult specimens (total length > 400 mm) caught in spring 2006, summer 2006, autumn 2006 and spring 2007 were used to calculate body-mass-indices (bmi). Bmi in spring 2006 was 1.1961–3.2414 (2.4348 +/ 0.6033), in summer 2006 it was 1.1057–3.1269 (2.2172 +/- 0.6146), in autumn 2006 it was 0.8454–2.2981 (1.4972+/-0.4257) and in spring 2007 it was 1.1872–2.8921 (1.9828 +/- 0.4901). Kruskal-Wallis statistics were performed to test data for significances (Fig. 11), which revealed that bmi differs significantly in respect to season ($P < 0.001$; Fig. 11 a) but not regarding to the sex of the respective specimens ($P < 0,189$. Fig. 11 b). To check if between seasons bmi differences are statistically significant, data for all four seasons were pair wise tested using Mann-Whitney *U*-test. These tests show, that differences between spring 2006 and autumn 2006 were highly significant ($P < 0.001$) as well as for summer 2006 and autumn 2006 ($P < 0.004$). All other pairs showed no significances.

To further evaluate the relationship of bmi between spring 2006 and autumn 2006 respectively summer 2006 and autumn 2006 Mann-Whitney *U*-tests were performed on data for males and females separately. As result, differences for males were significant between spring 2006 and autumn 2006 ($P < 0.001$) but not for females while between summer 2006 and autumn 2006 differences were significant for females ($P < 0.016$) but not for males. After FOWLER et al. (1998) Mann-Whitney *U*-test may be used with very low sampling units, but in that case there must be no overlap of observations between the two samples to reject H_0. This precondition of the test was met by the dataset for females with values for summer being 1.81–2.74 and for autumn 1.08–1.43, while it was not met by the dataset for males with values for spring being 1.99–3.24 and for autumn 0.85–2.30. Therefore we reject H_0 only for the females' dataset.

a.) Season: 1 = spring 2006; 2 = summer 2006; 3 = autumn 2006; 4 = spring 2007

	season	N	Mean Rank
bmi	1	12	44,08
	2	10	37,40
	3	12	15,67
	4	28	30,79
	Total	62	

Test Statistics(a,b)

	bmi
Chi-Square	16,193
df	3
Asymp. Sig.	,001

a Kruskal Wallis Test

b Grouping Variable: season

b.) Sex: 1 = male; 2 = female

	sex	N	Mean Rank
bmi	1	36	34,06
	2	26	27,96
	Total	62	

Test Statistics(a,b)

	bmi
Chi-Square	1,722
df	1
Asymp. Sig.	,189

a Kruskal Wallis Test

b Grouping Variable: sex

Fig. 11. Kruskal-Wallis test statistics testing body-mass-index data for significance regarding season (Fig. 11a) and sex (Fig. 11b).

DISCUSSION

Activity structures

As has been shown in this study *Uromastyx aegyptia microlepis* is highly seasonal, with this seasonality not being restricted to behavioral means of avoidance of temporarily unsuitable microenvironments but also to changes in the physical constitution of the animals (changes of bmi). The evaluation of thermoregulation in this species is not the primary objective of the present paper and will be discussed elsewhere (WILMS et al. in prep.). Nevertheless, the observed seasonality accounts to some degree to interactions between the thermal environment and the lizard and is therefore here briefly discussed.

Differences in temporal patterns of activity, the use of space, and body temperature relationships are not independent. Many lizards behaviorally regulate body temperatures by shuttling between sun and shade or hot and cold microenvironments to alter heat flux, by modifying posture to alter surface areas exposed to heat sources or sinks, and by regulating activity times (HUEY 1974, PIANKA 1986). These are well accepted paradigms of reptile ecology and especially true for extreme habitats like those inhabited by the studied *Uromastyx* at Mahazat as-Sayd.

The visibility profiles of *Uromastyx* at Mahazat as-Sayd show a bimodal structure in spring, early summer and to a lesser degree in summer combined with a general decrease of visibility from spring to summer. Visibility structure changes from a bimodal to an unimodal rhythm from summer to autumn reflecting changes in the availability of suitable thermal microhabitats. The visibility profile for autumn shows an overall very restricted level of visibility with a maximum occurring between 12.00 hrs and 15.00 hrs, then the hottest time of the day.

These results are in good accordance with the observations of AL-HAZMI et al. (2005) made in central Saudi Arabia (Al-Gassim region), with two activity peaks in spring (April) and summer (July) (9.00–11.00 hrs and 15.00–17.00 hrs in spring, 7.00–10.00 hrs and 16.00–18.00 hrs in summer) and only a single activity peak in autumn (mid October) (11.00–13.00 hrs). In this study observations were also conducted in early spring (February) showing that the animals have only one daily activity period in this season (11.00–15.00 hrs). After BOUSKILA (1986) the period with the highest activity is from March to September in a population of *Uromastyx a. aegyptia* in Israel, while from October to February only 70 % of the observed *Uromastyx* burrows showed signs of activity. The lowest levels of activity were recorded from December to Mid-February, were all observations of active specimens were made on clear and sunny days only.

In another study conducted by AL-JOHANY (2003) near Riyadh (Thumama; King Khalid Wildlife Research Center) an unimodal activity structure was observed in spring (May) starting between 9.00 and 10.00 hrs and ending around one hour before sunset. Summer activity (August) was found to be bimodal with one activity period starting 8.00–9.00 hrs until midday and another period from 15.00–16.00 hrs until sunset (18.30 hrs). We suggest, that the different spring activity profiles established in the present study compared with the result of AL-JOHANY (2003) might be explained by the different methodology used to assess activity. While in the present study a transect method was applied AL-JOHANY (2003) observed the animals from a hiding place within the study area, which probably lead to biased results by overestimating activity during midday by observing single actively roaming specimens. As has been shown in the present study, few specimens are visible above ground during midday but some of these show an extraordinary high activity by walking far from their respective burrow. All observed specimens being active during the hottest period of the day were adult. Adult *Uromastyx a. microlepis* have a body mass of up to 2.500 g and have therefore a higher thermal inertia than smaller conspecifics. This property is reducing the risk of overheating for large specimens and allows them a prolonged activity phase under unsuitable thermal conditions compared to smaller specimens.

Operative temperatures (T_e) for observation periods in spring 2007 and summer 2006 are available from three different microhabitats (sandy plain, gravel plain and 40 cm deep in the entrance of an *Uromastyx* burrow). There is only a slight difference regarding T_e, (average of all days with observations) between spring and summer with al-

Table 1. Operative temperatures of three different microhabitats in spring and summer in Mahazat as-Sayd (only temperatures between 07.00 hrs and 19.00 hrs were used for calculation).

	$T_{e\ (min,\ spring)}$	$T_{e\ (min,\ summer)}$	$T_{e\ (max,\ spring)}$	$T_{e\ (max,\ summer)}$	average $T_{e\ (spring)}$	average $T_{e\ (summer)}$
Sandy plain	27.8 °C	27.6 °C	54.4 °C	55.5 °C	45.3 °C	47.2 °C
Gravel plain	28.8 °C	28.4 °C	53.3 °C	54.8 °C	44.6 °C	46.4 °C
Burrow entrance	29.8 °C	35.1 °C	39.4 °C	38.1 °C	36.7 °C	37.2 °C

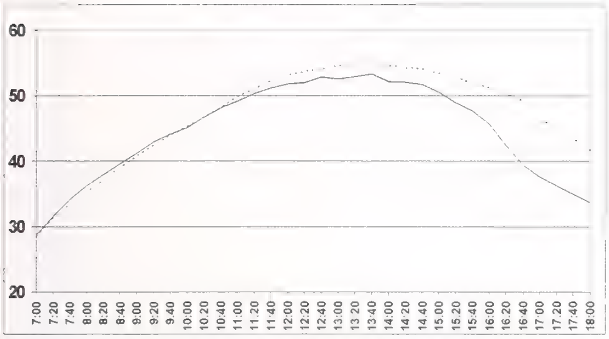

Fig. 12. Profiles of T_e in gravel plain in spring (solid line) and summer (dashed line).

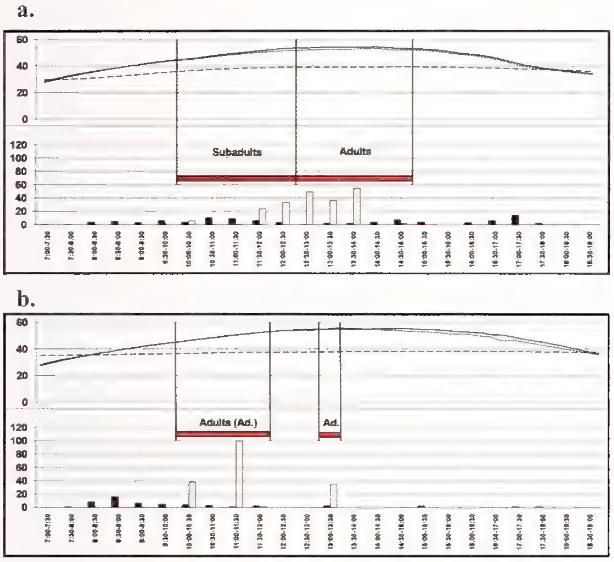

Fig. 13. Estimation of *Uromastyx* T_b based on average T_e; **a.** Spring; **b.** Summer; – – – T_e burrow entrance (approx. 40 cm deep); - - - -T_e gravel plain; ——T_e sandy plain

most identical minimum values but slightly higher maxima at summer (Tab. 1). The main observed differences lie in the temperatures of the *Uromastyx* burrow entrance and in the profiles of T_e in spring and summer (for the profile of T_e in the gravel plain see Fig. 12). During spring, temperatures in the entrance of the burrow differ between 7.00 hrs and 19.00 hrs about ten degrees centigrade while in summer this variation accounts only to three degrees. The profiles of mean $T_{e\ \text{gravel plain}}$ in spring and summer are quite similar until 10.40 hrs. After that time T_e rises faster in summer and reaches a higher maximum than in spring. Afternoon T_e in summer remains significantly higher until sunset (see Fig. 12).

Based on the combined visibility/activity profiles and the mean T_e for the respective seasons, body temperatures (T_b) for the first specimens seen outside of their burrows are estimated to be around 30–31 °C in spring and 33 °C in summer (because all specimens observed on the transects have been found in a gravel or in a mixed gravel/sandy microhabitat we suppose that T_b is within the range of $T_{e\ \text{sandy plain}}$ and $T_{e\ \text{gravel plain}}$). T_b estimates for specimens observed active far from their burrows are 44–52 °C for subadults and 48–54 °C for adults in spring and 47–55 °C for adults in summer (only adult specimens have been observed during summer).These temperature ranges were deduced using the actual measurements of T_e for each observed specimen (Fig. 13 gives an approximated visualization of these data!). These estimates are based on operative temperatures which reflect the interactions between biophysical and to some degree morphological factors influencing T_b of an ectotherm but lacking physiological (and behavioral) control (HERTZ et al. 1993) and therefore overestimate T_b, at least in the upper temperature range. The experimentally established critical maximum temperature (CT_{Max}) is 51°C for this taxon (AL-JOHANY 2003) and temperatures of 55 °C are lethal within 4–5 hours (EL-GOHARY & ASHOUR 1975), therefore it is suggested that *Uromastyx aegyptia microlepis* is able to control T_b by physiological and behavioral control mechanisms at least at high temperatures (data on T_b control based on semi continuous T_b measurements will be published elsewhere). It has to be pointed out, that preferred body temperatures change in respect to season, food composition and amount, hormonal status and other physiological traits and that therefore critical temperatures might also be subject to seasonal changes (PHILLIPS & HARLOW 1981, WOOD 1989, SEEBACHER & FRANKLIN 2005, TRACY et al. 2005).

Time windows during which operative temperatures in spring and summer would allow activity on a gravel plain far from the burrows were estimated for adult and subadult *Uromastyx* (Fig. 14) using the above listed T_b estimates (spring data of subadults were used to estimate time window during summer). The resulting diagrams show, that estimated time windows for subadults are considerably longer in spring and in summer compared to actually observed activity. In spring estimated time window is ca. four hours (ca. two hours at morning and two hours at afternoon), while observed activity is restricted to the morning totaling to ca. two hours. In summer estimated time window is ca. 3.5 hrs during two periods, one late morning and the other late afternoon, while observed activity was zero. For the adults, the estimated time window in spring is approximately 4.5 hrs and the period of observed activity is with ca. 4 hrs almost identical, while the estimated activity window for summer is about 6.5 hrs with the observed activity is only about two hours. The differences between the estimated and observed activity phases may be explained by the costs associated with thermoregulation, by other needs adversely influencing above ground activity like the necessity to maintain an adequate water balance and the seasonally different avail-

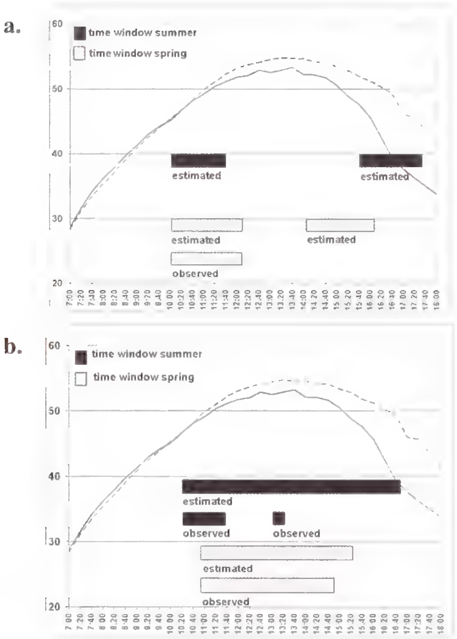

Fig. 14. Estimated time windows during which operative temperatures in spring (solid line) and summer (dashed line) would allow activity on a gravel plain far from the burrows for adult and subadult *Uromastyx*; **a.** for Subadults; **b.** for Adults.

ability of food sources. We suggest that the high activity in adults during spring is associated with reproduction; in this case the benefits of successful reproduction may outweigh the costs of thermoregulation.

Habitat selection

There is only one published study on habitat selection of *Uromastyx aegyptia* (Bouskila 1986). This study was carried out on the nominotypic subspecies (*Uromastyx a. aegyptia*) in southern Israel (near Hazeva Field Study Center, Arava) and focused on the following habitat parameters: habitat topography, soil type, distance to *Acacia* trees and orientation of burrow entrance.

Selected soil type at burrow location: After Bouskila (1986) *Uromastyx aegyptia* significantly prefers reg soil and avoids dry water courses, loose saline soil and sandy reg. This result is in accordance with the present study were medium gravel, fine gravel and coarse sand on the surface was significantly preferred. All of these three mentioned soil types can be subsumed as reg soil. Reg soil is characterized by a layer of closely packed stones over a layer of fine sediment several centimeters to meters thick (Breed et al. 1997). We suggest that this preference for reg soils is mainly because of the physical properties of this layer of fine sediments, providing a stable underground for the lizards to dig their burrows. Sandy soil [loose deep sand in old water courses (wadis) or sandy reg] might be disadvantageous to dig burrows in, because of its low stability and in the case of sandy reg because of the drifty sand being blown into the burrow entrance.

Orientation of burrow entrances: Bouskila (1986) did not find any evidence for a preference of specific orientation of the burrow entrances, which was principally confirmed by Al-Ogily & Hussain (1983) for *Uromastyx* burrows in the Riyadh Region. However these authors report a slightly higher number of burrow entrances oriented to the northeast. In the present study χ^2 analysis revealed a significant deviation of the observed distribution of burrow entrance directions from the expected distribution of burrow entrance directions, with the highest deviation from the expected value exists for burrow entrances directed to south-west and south-east (Fig. 8). One reason for this observation could be the prevailing wind direction, which is NE at 0–30° N. Unfortunately this suggestion can not be tested with actual data of wind directions in Mahazat as-Sayd because of a malfunctioning weather station during this study.

Selected vegetation coverage at burrow location: Vegetation coverage at burrow locations revealed to be significantly different compared to vegetation coverage frequency at randomly placed locations. Visibility/activity profiles of the present study are likely to explain this observed preference, because of the generally very high percentage of specimens seen in direct vicinity of their burrow entrance. Having a food source directly available near the retreat entrance may lower ecological stress for the lizards due to the supposedly relative low costs associated with foraging. Based on these observations it seems obvious, that for *Uromastyx a. microlepis* at least some vegetation in the vicinity is essential for the selection of a burrow location. One main difference between the results of the present study and those of Bouskila (1986) is the failure to demonstrate a significant relationship between burrow location and distribution of *Acacia* trees. In his study Bouskila found a significant correlation in the distance between *Uromastyx* burrow respectively random locations and the nearest *Acacia* tree. His medians of the distances were 21 m (burrow – *Acacia*) respectively 28 m (random location – *Acacia*). In the present study both medians are considerably lower (14.5 m) and even the median of all 206 registered burrows is comparably low (14.0 m). These findings raise again the question of the importance of *Acacia* for *Uromastyx* in Mahazat as-Sayd. We take our data as a high availability of *Acacia* for the lizards in Mahazat as-Sayd which we consider as a strong factor minimizing the need of an active selection of burrow locations in this particular respect. Nevertheless we regard *Acacia* trees as very important for the survival of *Uromastyx* providing food and opportunities for thermoregulation (Fig. 15).

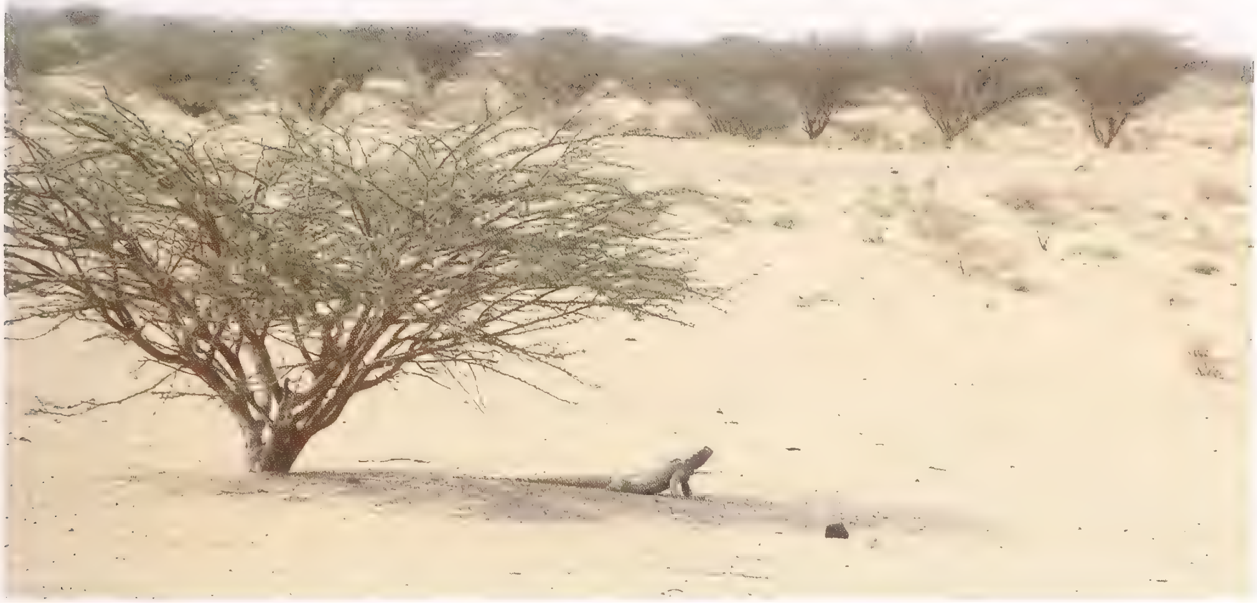

Fig. 15. Adult *Uromastyx* thermoregulating under an *Acacia* at Mahazat as-Sayd. Photo: T. Wilms.

Alternatively a second hypothesis explaining the "observed selection of locations" may be that *Uromastyx* is in fact a seed disperser and actively vegetates the area near the burrow entrance. The occurrence of seed dispersal through reptiles is well demonstrated (Godínez-Álvarez 2004, Valido & Olesen 2007). Spiny-tailed lizards defecate regularly near their own burrow which can be proven by the abundances of fecal pellets, and these pellets contain regularly seeds of different plant species. In Mahazat as-Sayd they consist in summer to a high degree of undigested seeds of *Acacia*. Al-Hazmi (2002) evaluated the amount of seeds in the stomach of 40 *Uromastyx a. microlepis* per season (spring, summer, autumn, winter) totaling 6.7 % (spring), 40 % (summer) and 48.2 % (autumn) of total organic matter, thus representing a significant portion of the total food intake. In winter no food at all was found in the stomachs. Therefore a study testing the effects of an intestinal passage on the germination of desert plant seeds and a possible impact of *Uromastyx* on the vegetation coverage would be highly beneficial to understand the ecology of the species and this desert community.

Seasonality of body weight

Seasonal changes in body weight of an *Uromastyx* species (*U. nigriventris*; nomenclature after Wilms et al. 2009) had already been evaluated by Grenot (1976) and Vernet et al. (1988). In this species changes in body conditions are quite pronounced and associated with seasonal differences in food availability, which is also related to rainfall distribution. Extracellular and intracellular fluid volumes vary widely during the year (Vernet et al. 1988). This is also the case in *U. a. microlepis* with significant differences in body mass indices between seasons and with marked differences in extracellular water in the body cavity (observation made during implantation of data loggers). This difference in seasonal body weight is most likely as in *Uromastyx nigriventris*, also attributed to the seasonality of food availability.

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Phylogeny of the genus *Agama* based on mitochondrial DNA sequence data

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Abstract. We present a preliminary phylogeny for 19 species of African *Agama* lizards based on a maximum likelihood phylogenetic analysis of 1,181 bp of mitochondrial DNA sequence data. Monophyletic radiations of species in East, South and West Africa are supported, as well as a clade containing two species (*A. doriae* and *A. sankaranica*) distributed across the Sahel region. West African populations of *A. agama* are paraphyletic with respect to *A. finchi* from westernmost Kenya, providing further evidence for a biogeographic corridor between West and East Africa. Populations of *A. agama* form four phylogeographic groups, which suggests that *A. agama* may be composed of multiple independent evolutionary lineages.

Key words. Africa, phylogeography, Systematics, biogeography, *Agama agama*.

INTRODUCTION

African lizards in the genus *Agama* are among the most diverse and widespread terrestrial squamates in Africa, making them an ideal group for testing biogeographic hypotheses and conducting comparative ecological and evolutionary studies. However, the robust phylogenetic framework for *Agama* that is needed to meet these goals is currently lacking. Constructing a phylogeny for *Agama* requires detailed investigations of phylogenetic relationships across multiple spatial and temporal scales. In general, the higher-level relationships within the Agamidae are poorly understood (MACEY et al. 2006), and dense sampling within *Agama* and other African and Asian taxa is necessary for testing the monophyly of and identifying the sister taxon to *Agama*. At the population level, several widespread and polytypic species, such as *Agama agama* in West Africa and *A. lionotus* in East Africa, have unclear species limits (BÖHME et al. 2005) and may be composed of multiple independent evolutionary lineages. These broadly distributed taxa pose some difficult species delimitation problems (WAGNER 2007; WAGNER et al. 2008a, WAGNER et al. 2008b) and require detailed phylogeographic investigations.

The goals of our collaborative research on *Agama* lizards are to combine our sampling efforts from separate biodiversity fieldwork programs in different countries across Africa to 1) infer a comprehensive molecular phylogeny for the genus *Agama*, 2) resolve species limits in widespread, non-exclusive taxa, 3) conduct phylogeographic investigations of the *A. agama* and *A. lionotus* complexes, and 4) describe new species, where warranted. In this paper, we present a preliminary phylogeny for the genus *Agama* based on an analysis of mitochondrial DNA sequence data (mtDNA). In addition, we investigate the phylogeography of *A. agama* across West Africa.

MATERIAL & METHODS

A total of 19 species of *Agama* were included in the phylogenetic analyses (Table 1). We included 15 specimens of *A. agama* from 10 countries across West Africa to investigate the phylogeographic relationships among populations. We selected four species from the Agaminae to represent outgroup taxa, including *Acanthocercus atricollis*, *Laudakia stellio*, *Trapelus mutabilis*, and *Xenagama taylori*. We rooted our phylogeny with *Laudakia stellio*, although we note that the higher-level relationships within the Agaminae are poorly understood (MACEY et al. 2000; 2006).

DNA was extracted from tissues following the PureGene Animal Tissue DNA Isolation Protocol (Gentra Systems, Inc). Two portions of the mitochondrial genome were PCR amplified and sequenced, including a small fragment of the 16S rRNA gene (16S) and a portion of the ND4 protein coding gene (ND4) and the adjacent histidine, serine, and leucine tRNA genes. Oligonucleotide primers used for PCR and sequencing are provided in Table 2. The 16S rRNA gene was PCR amplified for 30 cycles (95°C 30s, 58°C 30s, 72°C 50s) and the ND4 was amplified for 35 cycles (95°C 30s, 55°C 40s, 72°C 1 min). PCR products were purified using ExoSAP-IT (USB Corp.). Cycle sequencing products were ethanol precipitated, and then sequenced using an ABI 3730 automated sequencer.

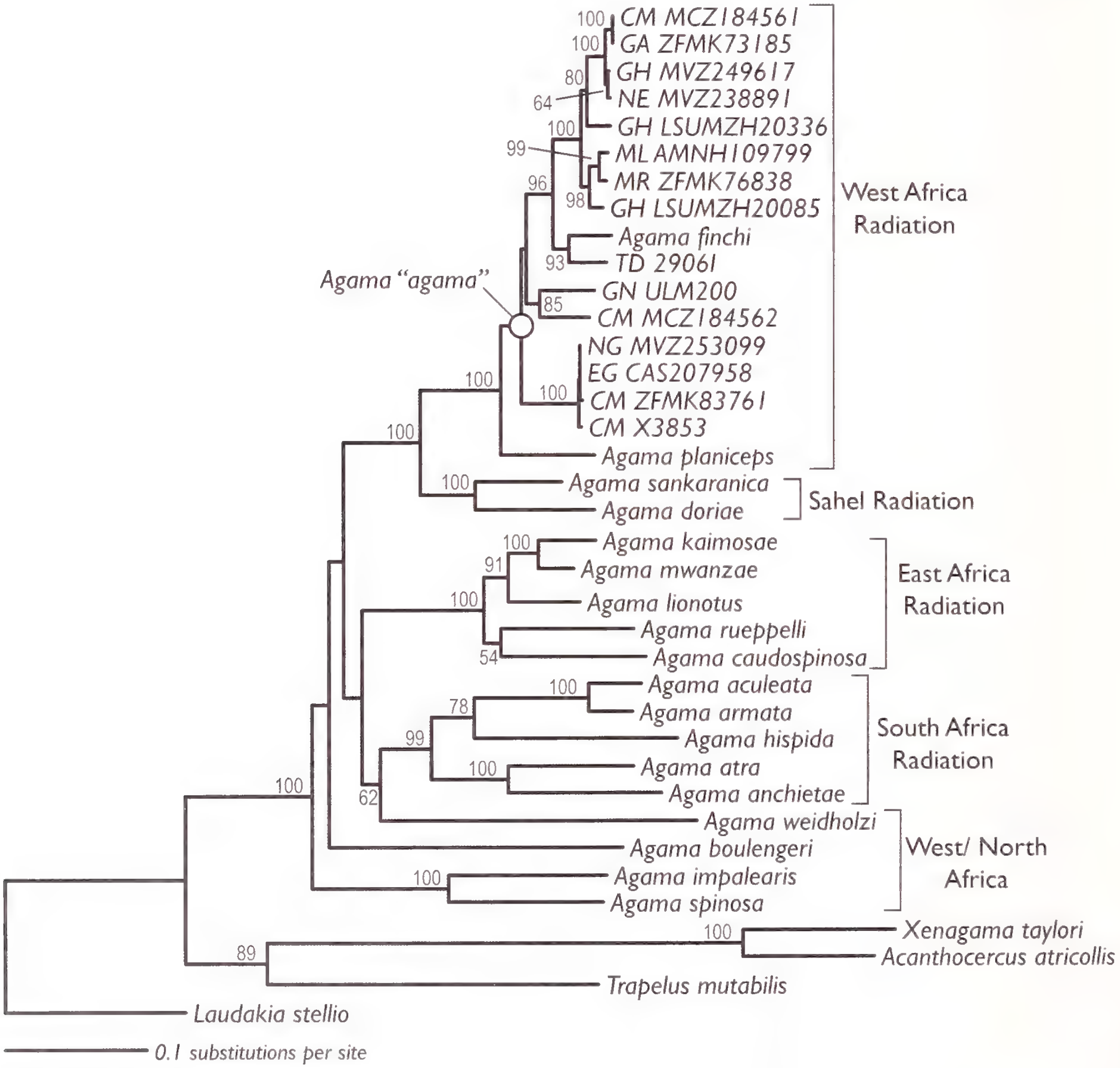
100
CM MCZ184561
100
GA ZFMK73185
80
GH MVZ249617
64
NE MVZ238891
100
GH LSUMZH20336
99
ML AMNH109799
MR ZFMK76838
96
98
GH LSUMZH20085
West Africa Radiation
Agama finchi
93
TD 29061
Agama "agama"
GN ULM200
85
CM MCZ184562
NG MVZ253099
EG CAS207958
100
100
CM ZFMK83761
CM X3853
100
Agama planiceps
100
Agama sankaranica
Agama doriae
Sahel Radiation
100
Agama kaimosae
91
Agama mwanzae
100
Agama lionotus
Agama rueppelli
54
Agama caudospinosa
East Africa Radiation
100
Agama aculeata
78
Agama armata
99
Agama hispida
100
Agama atra
Agama anchietae
South Africa Radiation
100
62
Agama weidholzi
Agama boulengeri
100
Agama impalearis
Agama spinosa
West/ North Africa
100
Xenagama taylori
89
Acanthocercus atricollis
Trapelus mutabilis
Laudakia stellio
0.1 substitutions per site

Fig. 1. Phylogenetic relationships within the genus *Agama* based on a maximum likelihood analysis of mtDNA sequence data using the GTR+Γ model of nucleotide substitution. Maximum likelihood bootstrap values ≥ 50% are shown.

Table 1. Voucher numbers and locality data for specimens used in the study. All sequences are deposited in GenBank (Accession Nos. GU128430 – GU128502). Voucher abbreviations are as follows: CAS, California Academy of Sciences; MVZ, Museum of Vertebrate Zoology; ZFMK, Zoologisches Forschungsinstitut und Museum; MCZ, Museum of Comparative Zoology; LSUMZ, Louisiana State University Museum of Natural Science; ULM, University of Louisiana at Monroe Museum of Natural History; AMNH, American Museum of Natural History; AMB, Aaron M. Bauer personal collection; specimen numbers beginning or ending with "X", "I", or "TR", personal collector numbers for authors from the Muséum national d'Histoire naturelle.

Species	Locality	Voucher
Agama aculeata	Botswana, Kgalagadi District	MVZ 198076
Agama agama	Cameroon	ZFMK 83761
Agama agama	Cameroon, Mende, monts Takamanda	X 3853
Agama agama	Cameroon, Yaounde	MCZ 184561
Agama agama	Cameroon, Yaounde	MCZ 184562
Agama agama	Equatorial Guinea, Bioko Island, Malabo	CAS 207958
Agama agama	Gabon, Barrage de Tchimbele	ZFMK 73185
Agama agama	Ghana, Greater Accra Region, Tesano	LSUMZ H20336
Agama agama	Ghana, Northern Region, Buipe	LSUMZ H20085
Agama agama	Ghana, Volta Region	MVZ 249617
Agama agama	Guinea, Diaragbela, Niger River	ULM 200
Agama agama	Mali	AMNH 109799
Agama agama	Mauritania, Selibabi	ZFMK 76838
Agama agama	Niger, Niamey	MVZ 238891
Agama agama	Nigeria, Cross River National Park	MVZ 253099
Agama agama	Tchad, Bol	2906 I
Agama anchietae	Namibia, Khorixas District	AMB 7582
Agama armata	Tanzania	ZFMK 84990
Agama atra	South Africa, Northern Cape Province	CAS 193435
Agama boulengeri	Mauritania, Nouakchott Dist.	MVZ 235764
Agama caudospinosa	Kenya, Naru Moru	ZFMK 83662
Agama doriae	Cameroon, Daré Ville	4218 X
Agama finchi	Kenya, Malaba	ZFMK 83653
Agama hispida	South Africa, Northern Cape Province	AMB 4800
Agama impalearis	Mauritania, Nouakchott District	MVZ 235766
Agama kaimosae	Kenya, Nandi	ZFMK 83660
Agama lionotus	Kenya, Nakuru	ZFMK 83646
Agama mwanzae	Kenya, Mara	ZFMK 82076
Agama planiceps	Namibia, Outjo Dist., Kamanjab	AMB 7638
Agama rueppelli	Somalia, Awdal Region	MVZ 241340
Agama sankaranica	Ghana, Volta Region	MVZ 249656
Agama spinosa	Djibouti, Dikhil	MVZ 236458
Agama weidholzi	Senegal	TR 481
Acanthocercus atricollis	Uganda, Rukungiri District	CAS 201726
Laudakia stellio	Turkey, Antalya Province	MVZ 230213
Trapelus mutabilis	Egypt	ZFMK 64395
Xenagama taylori	Somalia, Galbed Region	MVZ 241356

Contiguous DNA sequences were aligned and edited using Sequencher v4.8, and multiple sequence alignments were generated using Muscle v3.6 (Edgar 2004). The open reading frame for the ND4 gene was identified using MacClade v4.08 (Maddison & Maddison 2005). The 16S rRNA alignment included indel-rich loop regions that could not be aligned unambiguously and were excluded from the phylogenetic analysis. Phylogenetic relationships were inferred using maximum likelihood using RAxML v7.0.4 (Stamatakis 2008), and implemented the GTR+Γ model of nucleotide substitution. Support values for inferred relationships were estimated from 100 non-parametric bootstrap replicates.

RESULTS

The maximum likelihood analysis of the combined mtDNA sequence data (1,181 characters) supports the monophyly of the genus *Agama* (bootstrap = 100%; Fig. 1). The outgroup taxa *Xenagama taylori* and *Acanthocercus atricollis* form a strongly supported clade (bootstrap = 100%) that is sister to *Trapelus mutabilis*. Within *Agama*, a clade containing *A. impalearis* and *A. spinosa* is sister to all remaining *Agama*, although this relationship is not accompanied by strong support (bootstrap <50%; Fig. 1). Some regional species assemblages are monophyletic, including a clade of Southern African species (*A. aculeata*, *A. an-*

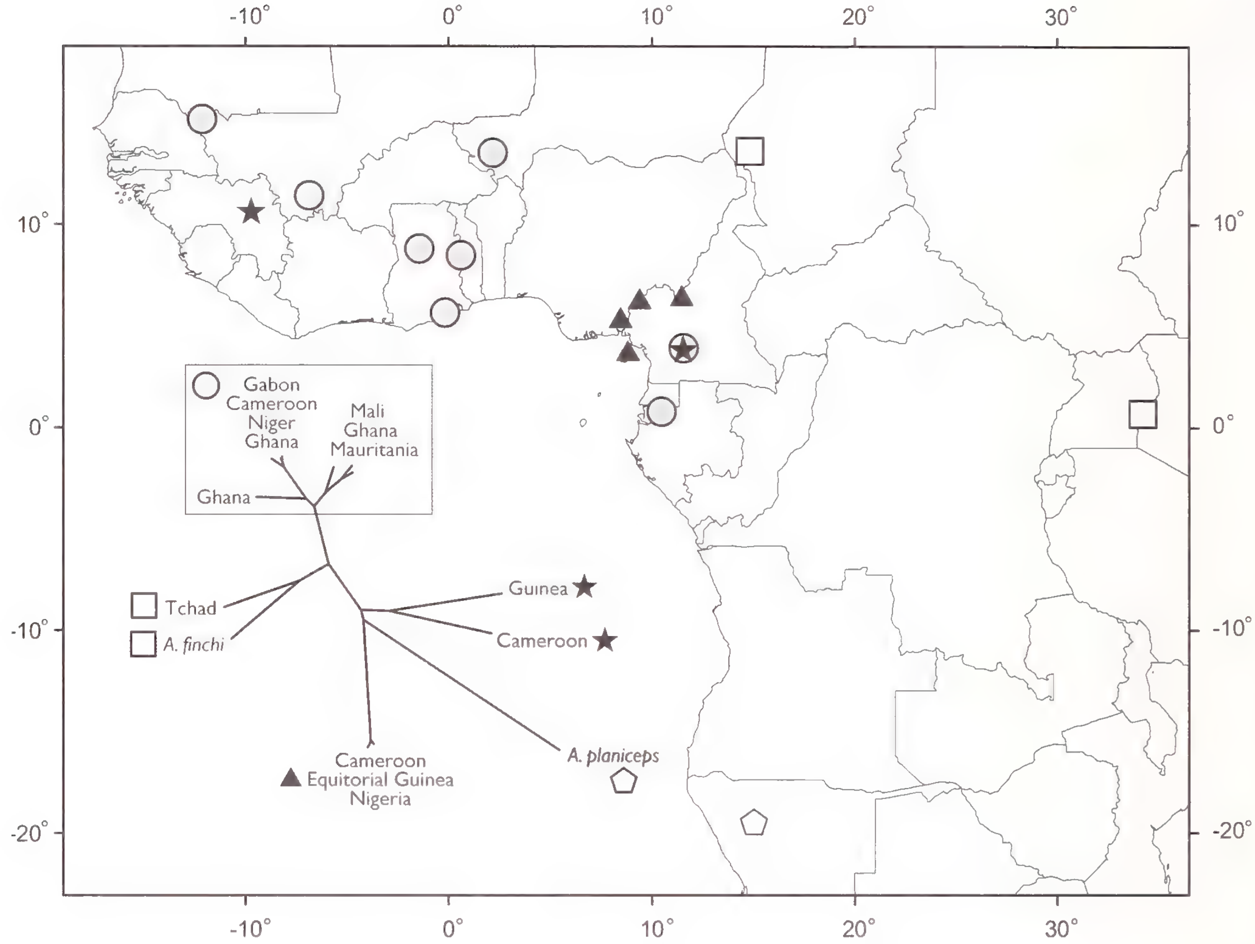

Fig. 2. Phylogeographic structure of *Agama agama* across sub-Saharan Africa. Samples of *Agama agama* are labeled by country in the unrooted phylogeny. The maximum likelihood phylogenetic analysis places *Agama planiceps* sister to *Agama agama*.

chietae, *A. atra*, *A. armata* and *A. hispida*) and a clade of East African species (*A. kaimosae*, *A. mwanzae*, *A. lionotus*, *A. caudospinosa* and *A. rueppelli*), each of which are strongly supported (bootstrap = 99% and 100%, respectively; Fig. 1). Strong support is also provided for a clade of species distributed across the Sahel region of sub-Saharan Africa, including *A. doriae* and *A. sankaranica* (bootstrap = 100%). *Agama planiceps* is sister to a clade containing all 15 specimens of *A. agama* and *A. finchi*, although this relationship is weak (bootstrap < 50%; Fig. 1). The interrelationships among these major clades are not supported by bootstrap values ≥ 50%, except for a strongly supported clade (bootstrap = 100%) containing the Sahel species (*A. doriae* and *A. sankaranica*) and *A. planiceps*, *A. agama*, and *A. finchi* (Fig. 1).

Populations of *Agama agama* in West Africa are paraphyletic with respect to *A. finchi* from westernmost Kenya (Fig. 1). Populations of *A. agama* form four phylogeographic groups (Fig. 2). The geographic proximity between samples is a poor predictor of phylogenetic relationships, and three of the four clades overlap spatially (Fig. 2). One of the most well sampled phylogeographic groups within *A. agama* extends across West Africa from Mauritania to Gabon (Fig. 2). Two other clades with broad distributions include a group extending from Guinea to Cameroon and another extending from Tchad to Kenya (*A. finchi*) (Fig. 2). Finally, a clade with a more restricted distribution includes populations from southeastern Nigeria, western Cameroon, and Bioko Island (Equatorial Guinea) (Fig. 2).

DISCUSSION

This study represents the first detailed molecular phylogenetic investigation of the genus *Agama*. Monophyletic radiations of *Agama* lizards occur in East Africa, South

Table 2. Primers used to amplify and sequence mitochondrial DNA.

Gene	Primers	Reference
16S	16Sf: CGCCTGTTTAACAAAAACAT 16sR: CCGGTCTGAACTCAGATCACGT	This study
ND4	ND4:CACCTATGACTACCAAAAGCTCATGTAGAAGC LEU: ACCACGTTTAGGTTCATTTTCATTAC	Arévalo et al. (1994)

Africa, the Sahel region, and even West Africa (Fig. 1), but reconstructing the biogeographic history of the group is impeded by several factors. First, the inter-relationships among the major lineages of *Agama* inferred by the mtDNA data are not accompanied by strong support, which would make any biogeographic scenarios based on the current phylogeny speculative. Second, our taxonomic coverage is not comprehensive and lacks approximately 10 species that are distributed throughout Africa. Finally, the sister taxon of *Agama* remains unclear. Despite these challenges, there are strong biogeographic signals in the current phylogeny (Fig. 1). For instance, the phylogenetic placement of *A. finchi* from western Kenya within the West African *A. agama* complex provides evidence for a biogeographic corridor between West and East Africa, a result that provides further evidence for a close biogeographic affinity between these regions (Wagner et al. 2008c). In addition, the close relationship between *A. planiceps* from Namibia and the West African *A. agama* complex provides support for a biogeographic connection between West and South Africa (Figs 1 and 2). This relationship is not surprising given the close similarity in morphology and colour pattern shared between these species (Böhme et al. 2005).

The intraspecific phylogeny for *Agama agama* highlights the taxonomic problems that this widespread taxon introduces to *Agama* lizard systematics. This species is paraphyletic with respect to *A. finchi* (Figs 1, 2) and appears to be composed of multiple distinct clades. The argument could be made that *A. finchi* should be synonymized with *A. agama* to retain a monophyletic *A. agama*, but *A. finchi* is clearly distinct based on morphology and coloration. The major phylogeographic groups found within *A. agama* based on mtDNA may represent distinct species, and represent a good starting point for testing species boundaries with multiple nuclear markers. Determining if gene flow is absent among these mtDNA groups is an important next step in resolving the systematics of the *A. agama* complex. The paraphyly of *A. agama* also underscores the need for additional detailed comparative morphological investigations that do not rely solely on adult male coloration characteristics (see Grandison 1968).

The phylogeographic relationships within the *Agama agama* complex exhibit a surprising amount of spatial overlap between clades. Phylogeographic studies of other *Agama* lizards, including *A. impalearis* (Brown et al. 2002) and *A. atra* (Matthee & Flemming 2002) recovered more typical phylogeographic patterns whereby populations formed geographically exclusive clades. The spatial overlap of mtDNA clades in the *A. agama* complex could be evidence of the presence of multiple distinct species, which co-occur throughout West Africa and are as of yet morphologically cryptic. Conversely, this spatial pattern could reflect the recent expansion of distinct lineages that were formerly restricted to exclusive geographic areas. Distinguishing among these different hypotheses of population history await the addition of more specimens from throughout West Africa and the collection of nuclear DNA data. This work is currently underway.

The collaborative nature of this research project is providing an opportunity to conduct detailed investigations of the phylogeny and phylogeography of *Agama* lizards than would have otherwise been impossible. Our current work benefits from having expanded taxonomic sampling and multiple individuals of each species, more detailed outgroup sampling, dense population sampling in *A. agama* and *A. lionotus* species, and the addition of nuclear DNA sequence data.

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A new species of *Bronchocela* (Squamata: Agamidae) from Nicobar Island

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Abstract. A new species of the genus *Bronchocela* from central part of Nicobar Islands is described. It is similar to *B. cristatella* but differs by having a red gular patch in males, fewer scale rows around midbody and only up to 3 dorsal body scales rows pointing upwards. It was found on seven islands of the central part of Nicobar but not in the northern or southern part of the archipelago. A colonization scenario of the Nicobar Islands by the genus *Bronchocela* is discussed. An arrival of an ancestor from Sumatra through the Great Channel is more probable than from north through the Ten Degree Channel by island hopping.

Key words. Squamata, Agamidae, Draconinae, *Bronchocela*, new species, India, Nicobar archipelago.

INTRODUCTION

The genus *Bronchocela* comprises nine species distributed in South East Asia, the Indo- Australian Archipelago, the Philippines and in western New Guinea (Wermuth 1967, De Rooiy 1915, Diong & Lim 1998, Hallermann 2005). Recently a taxonomic review of the genus was published including biogeographical data was given for each species (Hallermann 2005).

The Andaman and Nicobar Archipelagos are politically part of India. The herpetofauna of the Andaman Islands is considered to be of Chinese-Indian affinities, resulting from the connection of these islands to the mainland during late Pleistocene glaciations with sea level lowering of about 100 m. On the other hand, Nicobar Islands are considered to be of volcanic origin, with Indo-Malayan affinities (Das 1999). Its fauna established mainly through waif dispersal across the Great Channel from Sumatra. For the size of land area the islands of central Nicobar show the highest proportion of endemic snake species (Das 1999). Das (1999) summarized the history of herpetological exploration from its beginning in the middle of 19th century to the late 1990ies. The inventory of the Nicobar herpetofauna was relatively poor until the 1960ies. An expedition of the Zoological Survey of India in the 1960ies, however, increased our knowledge of the herpetofauna of the Nicobar Islands. Tiwary & Biswas (1973) described *Bronchocela danieli* from Great Nicobar. Indraneil Das, during several field trips between 1994 and 1998 discovered new species and country records and clarified problematic species records e.g. *Pseudocalotes archiducissae* Fitzinger, 1861, a nomen nudum, as *Bronchocela cristatella*. Other species such as *Calotes calotes* reported by Blyth (1863) as *C. ophiomachus* and by Smith (1935) as well as *Calotes jubatus* could not be verified to exist on Nicobar, since no voucher specimens exist (Das 1999, 2000). Das (1999) presented the currently most complete list of amphibians and reptiles from the Nicobar Islands. *Bronchocela cristatella* is known to occur on several islands in the north and south of Nicobar (Biswas & Sanyal 1980). *B. danieli* is restricted to Great Nicobar (see Fig. 1). S. P. Vijayakumar studied the herpetofauna of Nicobar Islands in his PhD Thesis. On several islands of the central Nicobar a lizard of the genus *Bronchocela* occurs which differs morphologically from the common *B. cristatella* and all other species of this genus. It was found on Katchal Island, Trincat Island, Camorta Island, Nancowry Island, Bompoka Island, Tarassa (Teressa) Island and Chowra Island.

It is more similar morphologically to *B. cristatella* than to *B. danieli*, but differs from it in several characters. A comparison with all other species of the genus shows that it represents a new species which I describe below.

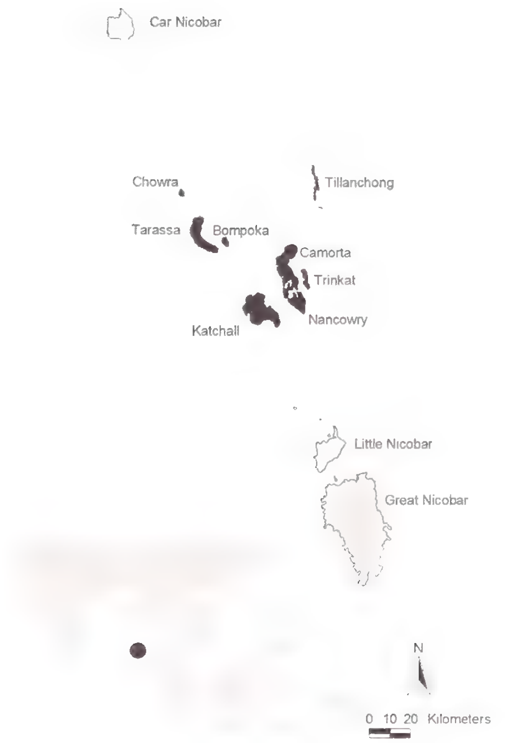

Fig. 1. Map of Nicobar Islands. Black coloured islands illustrate occurrence of *B. rubrigularis* sp. nov.

MATERIAL AND METHODS

The specimens examined for this study are listed in the appendix. Museum acronyms follow LEVITON et al. (1985). The following data were recorded: Snout-vent length (SVL), tail length (TL from cloaca to tip of tail, if tail was complete), head length (HL, between tip of snout and hind border of tympanum), head width (HW, at angle of jaw), number of supralabials (SL, on each side) and infralabials (IL, on each side), number of scale rows around midbody (M), hind limb length (HLL, from groin to tip of fourth toe, without claw), foot length (FL, without claw), as well as the ratios TL/SVL, HLL/SVL, HW/HL. In several specimens diameter of the tympanum and orbit, and the ratio of the two as well as the number of scales between the nasal scale and anterior border of orbit along the canthus rostralis, were also checked.

Bronchocela rubrigularis sp. nov.

Holotype. ZMH R09271 (Fieldnumber Tri 25) (see Fig. 2). An adult male collected by S.P. Vijayakumar on Trinkat Island, central Nicobar Islands, Nicobar in 2004.

Paratype. ZMH R09272 (Fieldnumber Kat 43). A subadult male, (Katchall Island), central Nicobar Islands, same collector as holotype. Six paratypes will be inventoried at ZSI: Fieldnumber BOM 21: Bomboka Island; Fieldnumber NAN 15: Nancowry Island; Fieldnumber CAM 76: Camorta Island; Fieldnumber TER 39: Teressa (Tarassa) Island); Fieldnumber CHO 05: Chowra Island: Fieldnumber BOM 27: Bomboka Island.

Diagnosis. A relative robust species with a SVL of 81–106 mm, and a long tail (280–377 mm (336–378 % of SVL). Tympanum large, more than half diameter of orbit, often dusky coloured, Ratio tympanum /orbit 0.74–0.89. Head covered above with small keeled scales, up to two slightly enlarged scales between orbit and tympanum. 7–10 supralabials and infralabials on each side. Canthus rostralis sharp, two small erect, compressed scales behind supraciliary edge. Nuchal crest formed by 7–10 lanceolate erect scales, bordered laterally by smaller erect scales, longest little longer than diameter of orbit. Dorsal crest smaller than nuchal crest, continues nuchal crest by a small gap. Mental wider than high, three postmentals, gular sac small in males, gular region covered with little enlarged keeled scales, smaller than ventrals.

Body scales mucronate, keeled, homogenous in 52–58 midbody scales. 1–3 uppermost scale rows next to dorsal crest pointing upward, 4–5 rows directed parallel, others scale rows directed downwards. Ventrals about two times larger than dorsals, strongly keeled. It can be distinguished from other congeners of the Nicobar Islands: from *B. cristatella* by a larger nuchal crest, only 1–4 upper scale rows pointing upwards (versus 5–10), and a red gular patch (white in alcohol) in males; from *B. danieli* by a larger tympanum (versus only half diameter of orbit) , longer fifth toe than fourth finger (versus fifth toe smaller than fourth finger) and only two times larger ventrals (versus five times larger)

Colouration. In life: Known for males only: body green to brown above, head light green to light brown, upper side of head sometimes mottled with red, tympanum black, orbit with a blue ring around eye, in some males body same colour as head (light brown), ventral side light to yellowish green with a V-shaped red patch on gular (Figs 3–6).

In alcohol: Males are dark brown to nearly black above, lighter brown on venter and on lower side of legs. A notably white, triangular patch (apex directed rostrally) on the gular region

Description of holotype (ZMH R09271, Fig. 2). Snout vent length 106.4 mm, tail length 377 mm, 355 % of SVL (original tail broken and separate), hind limb length from base of femur to tip of 4th toe (without claw) 88 mm, foot length to tip of fourth toe: 34 mm, length of toes (without claws) 1–5 in mm: 5.7 / 9.4/ 18.2 / 21.7 / 14.9, length of fingers 1–5 in mm: 3.8 / 7.3 / 13.2 / 13.0 / 7.7, head

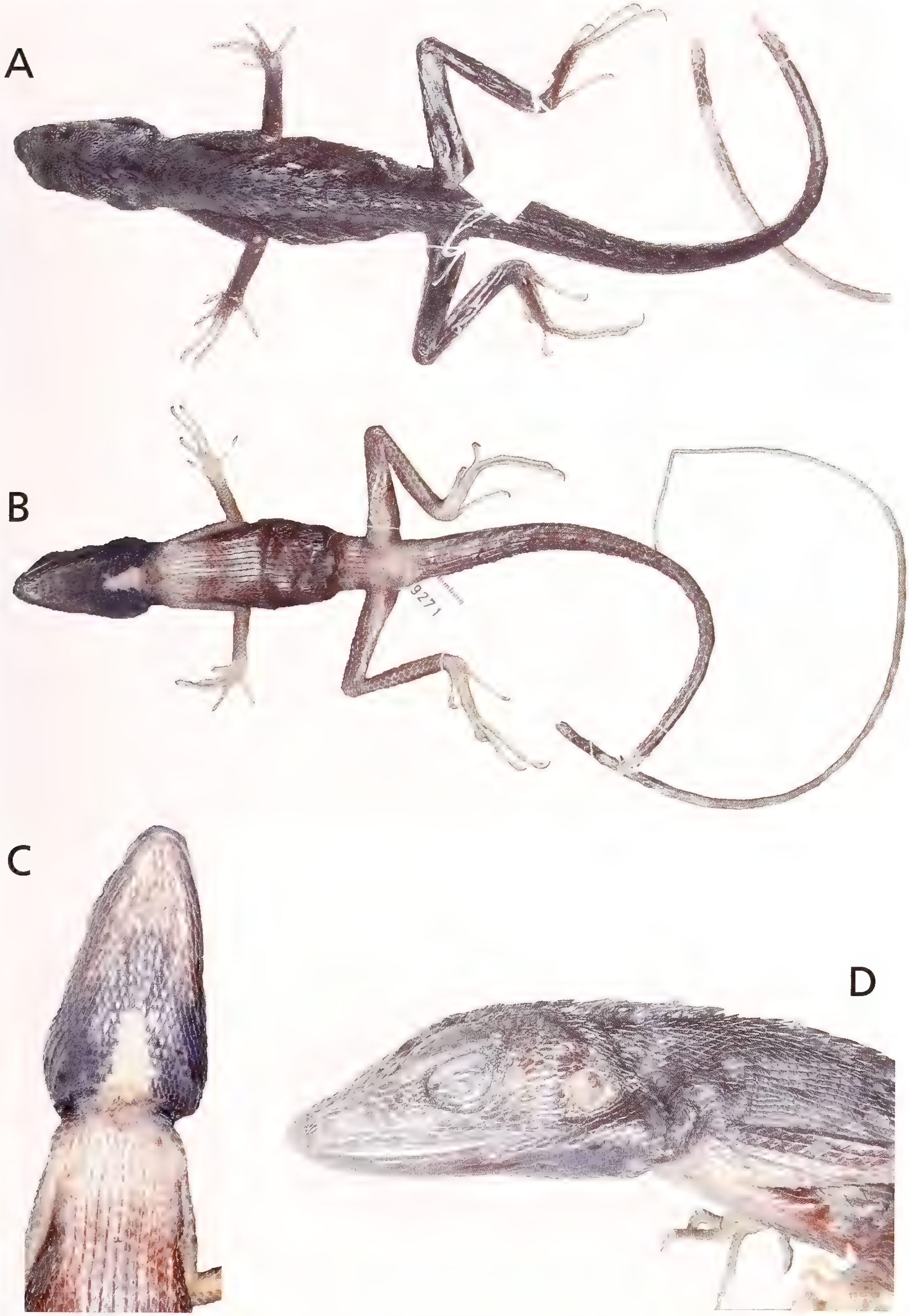

Fig. 2. Preserved holotype of *Bronchocela rubrigularis* sp. nov. (ZMH 9271). A= complete holotype in dorsal; B= complete holotype in ventral; C= head in ventral view; D= head in lateral view. Photo: J. Hallermann.

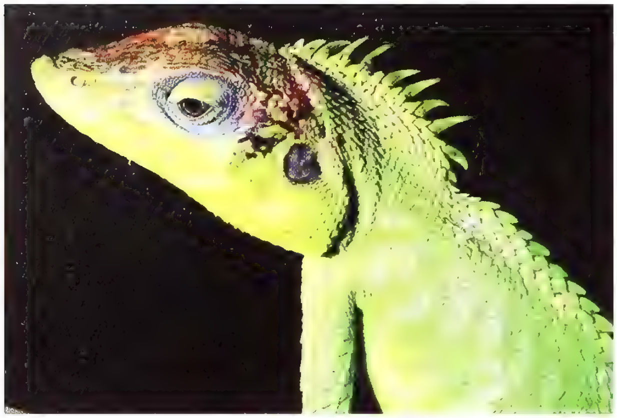

Fig. 3. *Bronchocela rubrigularis* male in life from Camorta Island. Photo: S.P. Vijayakumar.

width in temporal region 16.0 mm; head length from tip of snout to hind margin of tympanum: 30.4 mm. 9 upper labials and 8 lower labials on each side. Diameter of orbit 4.84 mm, diameter of tympanum 4.34 (ratio: tympanum/orbit 0.89). Head concave, covered above with small uniform keeled scales, two slightly enlarged scales intermixed on an upper line between orbit and tympanum 5 scales between nasal and anterior border of orbit along canthus rostralis. Mental wider than high, followed by three postmentals. Gular region covered by keeled scales, gular sac small, covered with little enlarged keeled scales, smaller than ventrals. A skin fold stretches from angle of mouth to insertion of foreleg. Nuchal crest formed by 10 lanceolate erect scales, bordered laterally by smaller erect scales, longest little longer than diameter of orbit. Middorsal scale row forming a small dorsal crest by triangular erect scales, which is lower than nuchal crest, separate from from it by a small gap. 54 scale rows around midbody, dorsal and lateral body scales small, mucronate, keeled; 2 uppermost scale rows directed upwards, next 5 below parallel to middorsal scale row, other dorsoventral scale rows directed downwards. Ventrals about two times larger than dorsals, strongly keeled. Limbs relatively strong, covered by keeled scales.

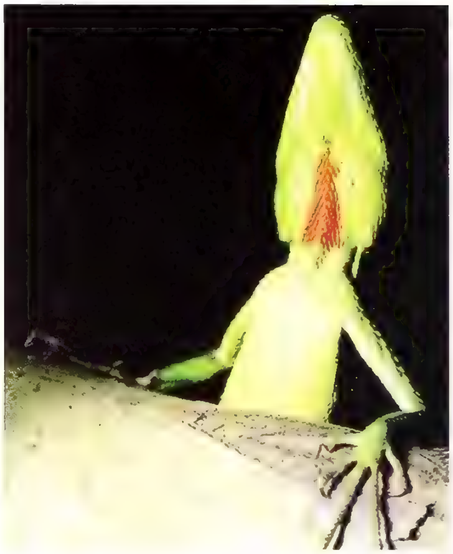

Fig. 4. *Bronchocela rubrigularis* same specimen as in Fig. 5, showing red gular patch. Photo: S.P. Vijayakumar.

Coloration. Coloration in life not known for holo- and paratype, but supposedly green body colouration. In alcohol (Fig. 2): upper side of body and head dark brown to almost black. A white gular patch, V-shaped, apex di-

Table 1. Measurements and scale counts of *Bronchocela rubrigularis* sp. nov.

specimen no	SVL	TL (% of SVL)	sex.	M	ear	orbit	SL/IL	HL.	HW	HW/ HL	HLL	FL	HLL/SVL %	remarks
ZMH R09271 holotype	106.4	377 (354)	m	54	4.34	4.84	9 9/8 8	30.4	16.0	0.52	88	34	82,7	Tail broken
ZMH R09272 paratype	80.3	304 (378)	m sad	58	3.51	4.39	9 9/8 9	23.3	13.0	0.55	68.6	28	85.4	
BOM 21	81.9	-lost	m	55	3,34	–	9 9/9 8	–	11.9	–	75.6		92.3	Nuchal crest 9
NAN 15	83.4	283 (339)	f	52	5.1	–	8 7/9 7	–	12.8	–	71.8		86.0	Eggs no gular patch
CAM 76	85.4	-lost	m	55	3.88	–	9 8/10 10			12.8	–	77.9	91.2	No patch ?
TER 39	85.3	287 (336)	m	56	2.8	–	9 10/9 10			12.7	–	78.2	91.6	Red patch
CHO 05	86.5	205 (reg.)	f	52	3.46	–	9 9/9 10		13.0	–	76.2		88.0	Pale gular patch
BOM 27	85.4	290 (339)	f	58	3.82	–	10 10/ 10 10		12.7	–	80.0		93.6	Eggs no gular patch

Snout-vent length (SVL), tail length (TL from cloaca to tip of tail, if tail was complete), head length (HL, between tip of snout and hind border of tympanum), head width (HW, at angle of jaw), number of supralabials (SL, on each side) and infralabials (IL, on each side), number of scales around midbody (M), hind limb length (HLL, from groin to tip of fourth toe, without claw), foot length (FL, without claw), as well as the ratios TL/SVL, HLL/SVL, HW/HL. In several specimens diameter of the tympanum and orbit.

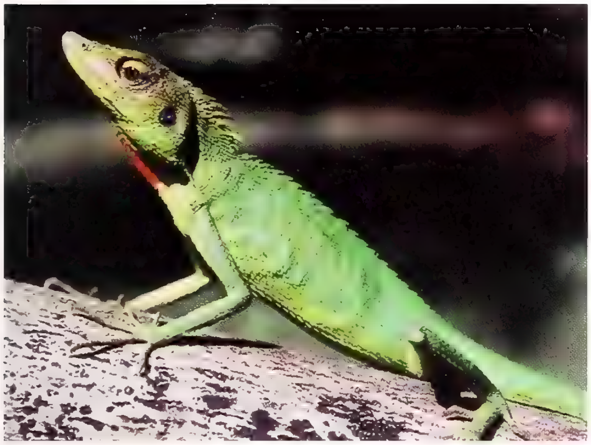

Fig. 5. *Bronchocela rubrigularis* male in life, from unknown locality in central Nicobar in green morph. Photo: S.P. Vijayakumar.

rected rostally. Tympanum dark, lower side of body between fore legs, underside of upper and lower legs and region around cloacae light brown, lower side of hands and foots whitish. Venter and lower side of tail brown.

Variations (see table 1). Females differ from the holotype by a lower nuchal crest, and by the lack of a red gular patch. One female has a pale gular patch and one subadult male has no gular patch. Tail length varies (280–377 mm [336–378 % of SVL]). Body colouration varies (see diagnosis). Body colouration (in alcohol) of venter and ventral side of legs and tail of paratype (ZMH R09272), subadult male, is very similar to the holotype. Scalation (see table 1) is similar. The nuchal crest is lower, no enlarges scales are present between orbit and tympanum.

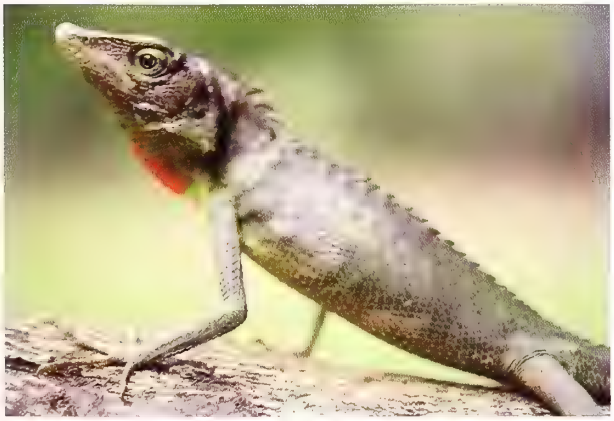

Fig. 6. *Bronchocela rubrigularis* male in life, from Trincat Island in brown morph. Photo: S.P. Vijayakumar.

Distribution. The new species is only known from the seven island of Central Nicobar (Fig. 1), and its distribution seems to be restricted to Central Nicobar.

Etymology. The species is named after its red gular (latin rubber = red, gula (feminin) = gular)

DISCUSSION

Bronchocela rubrigularis sp. nov. was observed and collected on several islands of Central Nicobar (Katchal Island, Trincat Island, Camorta Island, Nancowry Island, Bompoka Island, Tarassa Island and Chowra Island) while it is missing on the northern group (Carl island) and southern group of the Nicobar (Little and Great Nicobar). Pattern of distribution suggests that the new species is restricted to the central region of Nicobar. While *B. cristatella* occurs in the northern part, *B. danieli* was only recorded on Great Nicobar. From a biogeographical viewpoint it is important to know about geological history of Andaman and Nicobar Archipelago. Andaman and Nicobar are both parts of the Sunda Land and not of the Indian Subcontinent (DAS 1999). During glacial sea-level lowering in the Pleistocene (about 120.000 years ago) a land connection between Birma (Myanmar) and Andaman Archipelago existed. On the other hand, the Nicobar Islands were isolated during all times by the Great Channel from Sumatra in the southeast and by the Ten Degree Channel in the north. It is more plausible that a faunal colonization has occurred by dispersal through the Great Channel from Sundaland than by island hopping from north via Andaman since *Bronchocela* is missing on Andamar Island and Myanmar (DAS 1999). I can not yet estimate the time of arrival of a *Bronchocela* species on Nicobar nor can I resolve the genetic relationships as long as molecular data are still lacking

Acknowledgement. For loan of specimens we thank, Ivan Ineich (MNHN), I am very grateful to Wolfgang Böhme (ZFMK) for reading and providing helpful comments on an earlier version of the manuscript, and Indraeil Das (Kota Samarahan, Malaysia*)* for providing a map of Nicobar Islands. S. P. Vijayakumar provided me two specimens for description, and some incomplete measurement data of six specimens of the same species but no catalog numbers. Also, data on colouration of these specimens and habitat notes are still lacking.

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Appendix: Material examined

Bronchocela rubrigularis. India: Nicobar Island: Trincat Island (ZMH R09271 (field no Tri 25) holotype); Katchin Island (ZMH R09272 (field no Kat 43) paratype), Bompoka Island (No catalogue no. (field No. BOM 21)); Nancowry Island (No catalogue no. (field NAN 15)); Camorta Island (No catalogue no. (field no. CAM 76)), Teressa (Tarassa) Island (No catalogue no. (field TER 39)); Chowra Island (No catalogue no. (field no. CHO 05)), Bompoka Island (No catalogue no. (field no. BOM 27. ***Bronchocela cristatella.*** Indonesia: Sumatra: Serdang 3°30'N 98°50'E (ZMH R0608; R05602-3); NE Sumatra: Kwalu (ZMH R05623), Sumatera Barat: Indrapura 2°04'S,100°56'E (ZMH R05600);Tandjong: Padang District 0°38'S 100°52'E (ZMH R05624); Environs of Pispis 3°10'N,99°01'E, mountain region (ZMH R04928-9); Pulo Weh Island: Sabang (ZMH R05625); Indrgiri: Riau: Sungei Lalak 0°27'S 102°59'E (ZMH R06075-6); Nias Island (ZMH R04893-5).

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Studies on African *Agama* VII. A new species of the *Agama agama*-group (Linnaeus, 1758) (Sauria: Agamidae) from Cameroon & Gabon, with comments on *Agama mehelyi* Tornier, 1902

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Abstract. In the course of recent taxonomic studies in the African Agamidae the West African species were examined and new species have been identified. In this publication a new species of the genus *Agama* Daudin, 1802 is described from Cameroon and Gabon. Males of the new species differ from all other known *Agama* in the unique combination of the reticulate colouration of the throat and the blue tip of tail. It is compared with the other Cameroonian members of the genus and several other *Agama* species from Africa. Additionally, the status of *Agama mehelyi* Tornier, 1902, only known from its holotype, is discussed.

Key words. Reptilia: Sauria, Agamidae, *Agama* sp. n., *Agama mehelyi*, Africa, Cameroon, Gabon, morphology, taxonomy.

INTRODUCTION

After research activities on the genus *Agama* Daudin, 1802 in the last few years many species were described, synonymised or revalidated (Padial 2005, Wagner 2007, Wagner et al 2008a, Wagner et al. 2008b). Currently, the genus contains 35 recognised species, but preliminary results (especially from the West African clade of the genus) show several cryptic taxa within the *Agama agama* (Linnaeus, 1758) complex. Therefore, many populations are under investigation and especially vouchers from Cameroon were of special interest to the authors, because the type locality of *Agama agama* has been restricted to this country.

However, until recently it was not possible to characterize the 'true' *Lacerta agama* Linnaeus, 1758, because the syntypes illustrated in Seba (1734) are not available and the proposed type material in the Museum Adolphi Friderici collection of the Naturhistoriska Riksmuseet (= The Swedish Museum of Natural History) is not identical with the illustrated specimens. Wagner et al. (2009b) clarified this situation by designating a neotype (ZFMK 15222) from Cameroon. The authors followed Mertens (1938) who restricted the erroneous type locality 'America' of *Agama agama* to Cameroon but failed to fix this decision, according to article 76 of the Internatio-nal Code of Zoological Nomenclature (ICZN 1999) by designating a lecto- or neotype. Now, after the proper de-finition of a neotype (Wagner et al. 2009b), a taxo-nomic revision of this species group is possible and the already recognised new species can be described.

Chirio & LeBreton (2007) listed seven species of *Agama* for Cameroon: *Agama a. agama* (Linnaeus, 1758); *Agama doriae benueensis* Monard, 1951; *Agama gracilimembris* Chabanaud, 1918; *Agama mehelyi* Tornier, 1902; *Agama paragama* Grandison, 1968; *Agama sankaranica* Chabanaud, 1918 and *Agama sylvanus* MacDonald, 1981. In the adjoining countries of Cameroon, no other than the above mentioned *Agama* species occur (Wagner, unpubl. data) but Chirio & LeBreton (2007) also identified four probable new *Agama* species from Cameroon and one of them (*Agama* sp. 1) turned out to be identical with the new species recognized by us before, and we describe it herein.

MATERIAL & METHODS

The type material of the new species is deposited in the Zoologisches Forschungsmuseum A. Koenig, Bonn, Zoologisches Museum für Naturkunde, Berlin and the Muséum d'histoire naturelle, Geneva. It was compared with vouchers from Cameroon and other African countries housed in those collection (see appendix) and with data from literature (GRANDISON 1968, CHIRIO & LEBRETON 2007).

Measurements were taken with a digital calliper to the nearest of 0.1 mm. Measurements and scale counts were done following GRANDISON (1968), MOODY (1980) and MOODY & BÖHME (1984).

Molecular data were collected to examine sequence variation between the new species and its morphologically closest relatives. A portion of the mitochondrial 16S rRNA gene of the holotype of the new species (ZFMK 87698; GenBank accession number: GU133316), a series of other specimens of the new species (no voucher; GenBank accession number: GU133315; ZFMK 73241; GenBank accession number: GU133317; ZFMK 75376; GenBank accession number: GU133318; ZFMK 83762; GenBank accession number: GU133319; ZFMK 83766; GenBank accession number: GU133320), as well as the proposed neotype of *Lacerta agama* (ZFMK 15222; GenBank accession number: GU133323) from northern Cameroon, *Agama sankaranica* (ZFMK 84992; GenBank accession number: GU133327) from an unknown locality, *Agama paragama* (ZFMK 15244; GenBank accession number: GU133321) from Cameroon, Waza, Logone et Chari, *Agama agama africana* (ZFMK 73845, ZFMK 73846; GenBank accession numbers: GU133311, GU133312) both from Senegal, Dakar-Bel Air, *Agama agama* ssp. (MHNG 2689.53; GenBank accession number: GU133310) from Benin, *Agama boueti* (ZFMK 80057) from Mauritania, 30km NW of Rosso, and *Agama finchi* (ZFMK 83652; GenBank accession number: GU133314) from Kenya, Malaba (type locality) were sequenced. Sequences for *Agama planiceps* (GenBank accession number: AF355476) and *Agama castroviejoi* (GenBank accession number: AY522929) were added to the dataset from already published sequences (MATTHEE & FLEMMING 2002, PADIAL 2005). *Acanthocercus atricollis* (ZFMK 41748; GenBank accession number: GU133322 Botswana, Gaborone) was chosen as outgroup.

DNA was extracted using QuiAmp tissue extraction kits (Quiagen) or a modified Chelex-Protocol (WALSH et al. 1991, SCHMITZ 2003). The primers 16sar-L (light chain; 5' – CGC CTG TTT ATC AAA AAC AT – 3') and 16sbr-H (heavy chain; 5' – CCG GTC TGA ACT CAG ATC ACG T – 3') of PALUMBI et al. (1991) were used to amplify a portion of the mitochondrial 16S ribosomal RNA gene. PCR cycling procedure was as described in SCHMITZ et al. (2005). PCR products were purified using Quiaquick purification kits (Quiagen). Sequences were obtained using an automatic sequencer (ABI 377). Sequences were aligned using ClustalX (THOMPSON et al. 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (HALL 1999); this resulted in a total of 505 bp for the chosen section of the 16S gene. Phylogenetic trees were calculated in the program Paup* 4.0b10 (SWOFFORD 2002) using the neighbor-joining algorithm (NJ) and bootstrapping with 20000 pseudo-replicates to estimate node support as well as with a maximum parsimony approach (heuristic search with TBR branch swapping, stepwise random addition with 100 replicates, bootstrapping with 2000 pseudo-replicates). Paup* 4.0b10 was also used to compute the uncorrected pairwise distances for all sequences.

The following measurements and scale counts were partly used to compare the different species (see table 1): Snout-vent length (SVL): measured from mental scale to cloaca; tail length (TL): measured from cloaca to tip of tail; head length (HL): measured from jugale to rostral scale; head height (HH): measured at the jugal-postorbital region; head width (HW): measured across the jugal-postorbital region just anterior to the external auditory meatus; Midbody scales (MS): scale rows around midbody; vertebral scales (VS): number of midline vertebral scales, counted from midpoint of pectoral region to midpoint of pelvic region; dorsal scales (DS): number of midline longitudinal dorsal scales, counted from midpoint of pectoral region to cloaca; cloacal pores (CP).

RESULTS & DISCUSSION

Species of the genus *Agama*, unlike chameleons, the sister taxon of the Agamidae (e.g. MACEY et al. 2000), are very conservative in body form, without developing ornaments like e.g. horns or ear laps. Only in some species body ornamentations like enlarged nuchal or tail crest are present. If one takes into consideration the results from the chameleons (ZIEGLER & BÖHME 1997; BÖHME & ZIEGLER 2008), where morphologically similar species show high variations in hemipenis structures, a similar situation in the Agamidae could be expected. In contrast, preliminary results (BÖHME 1988; WAGNER et al., unpubl. data) show a high level of homoplasy and conservative morphology in the hemipenis structures in the genus *Agama*. Consequently, beside from body form and hemipenis structure, there must be another mechanism of species recognition. A pre-mating mechanism was identified by several authors (LOVERIDGE 1933, THYS VAN DEN AUDENAERDE 1963, MCLACHLAN 1981, BÖHME et al. 2005,

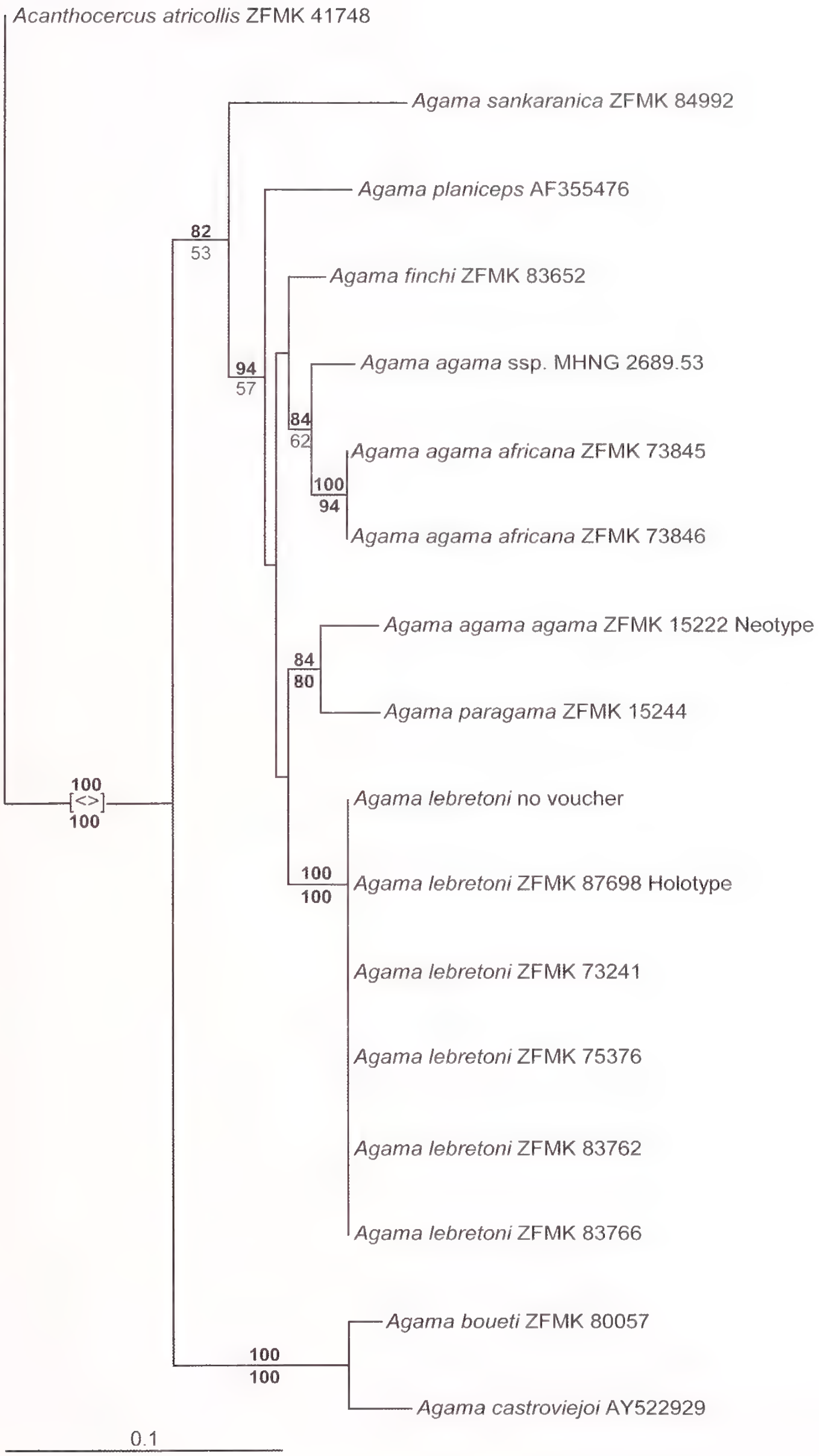
Acanthocercus atricollis ZFMK 41748
Agama sankaranica ZFMK 84992
Agama planiceps AF355476
Agama finchi ZFMK 83652
Agama agama ssp. MHNG 2689.53
Agama agama africana ZFMK 73845
Agama agama africana ZFMK 73846
Agama agama agama ZFMK 15222 Neotype
Agama paragama ZFMK 15244
Agama lebretoni no voucher
Agama lebretoni ZFMK 87698 Holotype
Agama lebretoni ZFMK 73241
Agama lebretoni ZFMK 75376
Agama lebretoni ZFMK 83762
Agama lebretoni ZFMK 83766
Agama boueti ZFMK 80057
Agama castroviejoi AY522929
82
53
94
57
84
62
100
94
84
80
100
100
100
[<>]
100
100
100
0.1

Fig. 1. Phylogenetic tree based on 505 bp of the mitochondrial 16S rRNA gene. Values above the nodes represent neighbour-joining bootstrap (20000 pseudo-replicates) values in percent while the values blow the nodes are the corresponding maximum parsimony supports. Significantly supported values are in bold. Values below 50% are not shown. The branch length from the outgroup (*Acanthocercus*) to the ingroup (*Agama*) has been shortened for visual purposes.

Table 1. Uncorrected p-distances for 505 bp of the mitochondrial 16SrRNA sequences used in this study.

	Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	*Acanthocercus atricollis* ZFMK 41748	-																
2	*Agama agama* ssp. MHNG 2689.53	0.1902	-															
3	*Agama agama agama* ZFMK 15222 (Neotype)	0.2073	0.0468	-														
4	*Agama agama africana* ZFMK 73845	0.1832	0.0200	0.0447	-													
5	*Agama agama africana* ZFMK 73846	0.1832	0.0200	0.0447	0.0000	-												
6	*Agama boueti* ZFMK 80057	0.2000	0.1012	0.1067	0.1011	0.1011	-											
7	*Agama castroviejoi* AY522929	0.2102	0.1087	0.1166	0.1087	0.1087	0.0241	-										
8	*Agama sankaranica* ZFMK 84992	0.1949	0.0722	0.0783	0.0701	0.0701	0.1193	0.1251	-									
9	*Agama finchi* ZFMK 83652	0.1931	0.0301	0.0317	0.0220	0.0220	0.0971	0.1047	0.0700	-								
10	*Agama lebretoni* sp. n. (no voucher)	0.1932	0.0381	0.0381	0.0381	0.0381	0.0931	0.1007	0.0784	0.0301	-							
11	*Agama lebretoni* sp. n. ZFMK 87698 (Holotype)	0.1932	0.0381	0.0381	0.0381	0.0381	0.0931	0.1007	0.0784	0.0301	0.0000	-						
12	*Agama lebretoni* sp. n. ZFMK 73241	0.1932	0.0381	0.0381	0.0381	0.0381	0.0931	0.1007	0.0784	0.0301	0.0000	0.0000	-					
13	*Agama lebretoni* sp. n. ZFMK 75376	0.1932	0.0381	0.0381	0.0381	0.0381	0.0931	0.1007	0.0784	0.0301	0.0000	0.0000	0.0000	-				
14	*Agama lebretoni* sp. n. ZFMK 83762	0.1932	0.0381	0.0381	0.0381	0.0381	0.0931	0.1007	0.0784	0.0301	0.0000	0.0000	0.0000	0.0000	-			
15	*Agama lebretoni* sp. n. ZFMK 83766	0.1932	0.0381	0.0381	0.0381	0.0381	0.0931	0.1007	0.0784	0.0301	0.0000	0.0000	0.0000	0.0000	0.0000	-		
16	*Agama paragama* ZFMK 15244	0.2124	0.0443	0.0296	0.0423	0.0423	0.1098	0.1153	0.0827	0.0341	0.0382	0.0382	0.0382	0.0382	0.0382	0.0382	-	
17	*Agama planiceps* AF355476	0.2054	0.0471	0.0472	0.0426	0.0426	0.0940	0.0987	0.0760	0.0359	0.0449	0.0449	0.0449	0.0449	0.0449	0.0449	0.0448	-

WAGNER 2007, WAGNER et al. 2008a, 2008b) as the colouration of head, throat, forelimbs and tail of nuptial males. In conclusion, the colouration of dominant males and, sometimes, of pregnant females can be used for the identification of the different species in the genus *Agama*, but not for analysing phylogenetic relationships. One of the main characters is the colouration pattern of the throat (JACOBSON 1992; MCLACHLAN 1981; WAGNER 2007; WAGNER et al. 2008a, 2008b). Dominant males present their throat, head and forelimbs in a behavioural context to other adult male competitors and, especially, females. Consequently, these characters are useful to distinguish different species and to compare the herein described new species with closely related taxa. Therefore, we compare the new species not only in pholidosis and morphometrics with other *Agama* species, chiefly with that ones occurring in Cameroon, but we turn our attention especially to the colouration of dominant males.

Genetics: For the genetic dataset both phylogenetic calculation methods completely agree in the topology of the recovered phylogenetic tree (fig. 1), and only differ in the degree of support recovered for the individual nodes.

The phylogenetic tree is rather well resolved with three major groups apparent. The first and basal fully supported clade includes *Agama boueti* and the only recently described *A. castroviejoi* (NJ: 100/MP: 100). The position of this clade corresponds well with the positioning of other extreme West- or North African taxa in the more complete phylogeny of LEACHÉ et al. (2009), therefore it is likely that these two taxa are part of a more comprehensive north-western clade within the genus *Agama*. The second clade is only well supported by the neighbour-joining analysis and is represented in this tree by a single species (*Agama sankaranica*), and represents the "Sahel Radiation"-clade identified by LEACHÉ et al. (2009).

The third and largest clade includes a basal unresolved polytomy because the phylogenetic position of *A. planiceps* and *A. finchi* could not be resolved with the used gene fragment. But here the three well supported subclades are of importance: the first subclade includes the proposed neotype of *Agama a. agama* and the closely related *A. paragama* (NJ: 84/MP: 80), the second subclade includes the two Senegalese vouchers of *Agama a. africana* as well as a specimen from Benin (NJ: 84/MP: 62), while the third clade fully supported clade (NJ: 100/MP: 100) contains all the included vouchers of "*Agama* sp. n.".

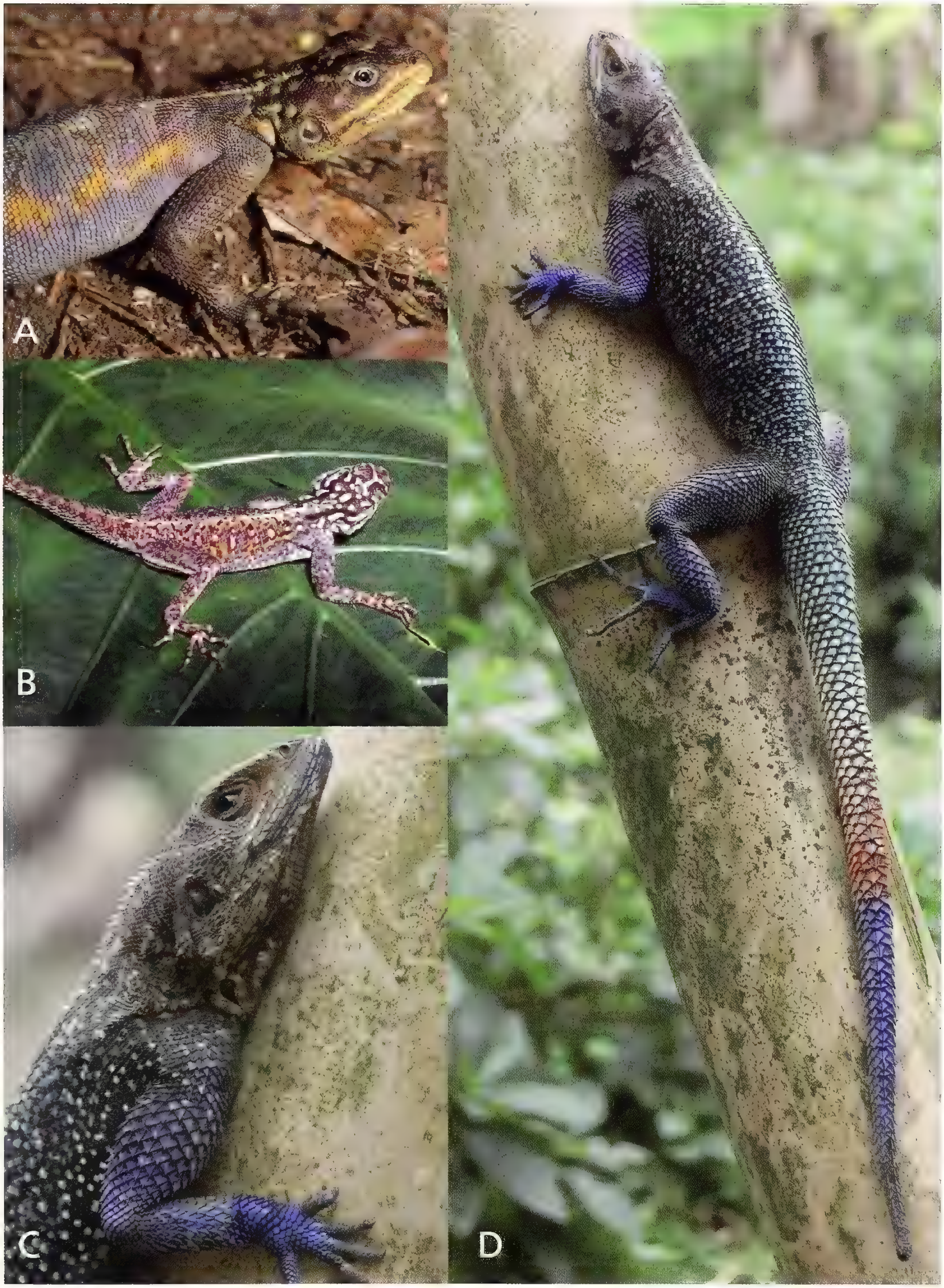

Fig. 2. Images of *Agama lebretoni* sp. n. alive: A. Pregnant female of *Agama lebretoni* sp. n. from Mt. Nlonako, Cameroon (ZFMK 75376) | B. Non-pregnant female of *Agama lebretoni* sp. n. from Nyasoso, Mt. Kupe, Cameroon | C. Close-up of the head of the living holotype of *Agama lebretoni* sp. n. from northeast of Mamfe, Mukwecha, Amebisu, Cameroon. | D. Holotype of *Agama lebretoni* sp. n. in life

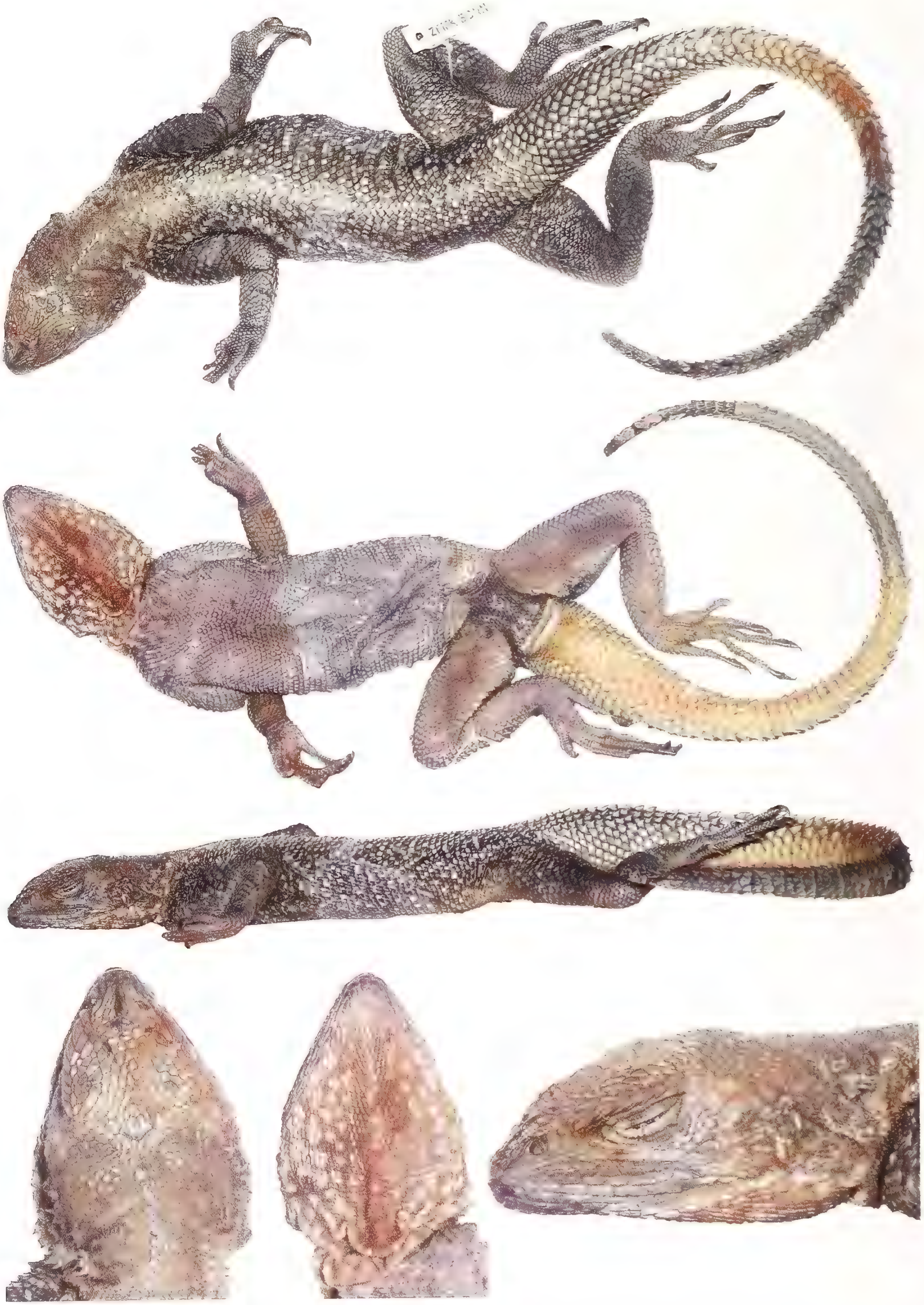

Fig. 3. Preserved holotype of *Agama lebretoni* sp. n. (ZFMK 87698) from nordeast of Mamfe, Mukwecha, Amebisu in Cameroon.

Table 1 summarizes the uncorrected p-distances for the used gene fragment. The neotype of *Agama a. agama* shows only a comparatively low genetic difference (2.96%) to its sister taxon *A. paragama*, while it differs from its western 'subspecies' *Agama a. africana* by 4.47% and from *Agama* sp. n. by 3.81%. The latter two species are separated by an equal genetic distance (3.81%). These distances are of similar magnitude than to other well established species within this large clade (*A. a. agama* [neotype]-*A. planiceps* 4.72%; *A. a. agama* [neotype]-*A. finchi* 3.17%; *A. finchi*-*A. planiceps* 3.59%). Regarding the genetic distances of vouchers which we morphologically confirmed to be members of the same taxon we find them to be genetically identical to each other; this is true both for the two *Agama a. africana* specimens as well as for all six vouchers of in the third subclade (*Agama* sp. n.).

The identified genetic structure (low to non-existent intra-clade distances and moderately higher but more or less equidistant inter-clade distances) is typical for rather young radiations. Our genetical analyses therefore supports the idea of previous studies (e.g. Wagner 2007; Wagner et al. 2008a, 2008b) that many of the previously recognised species in the genus *Agama* in reality comprise of several taxa, which are often very difficult to separate on the basis of external morphology alone, and the same now holds true for *Agama agama* sensu lato.

The inclusion of morphologically well established species (*A. planiceps*, *A. finchi*, *A. paragama*), which show nearly equal genetic distances to the neotype of *A. a. agama* prove that the uncovered distance of *Agama* sp. n. to all other closely related congeners confirms the specific distinctness of *Agama* sp. 1 and together with morphological evidence (see below) warrants the formal recognition of this species.

Agama lebretoni sp. n.

Holotype (figs. 2c–d, 3, 4.1)

ZFMK 87698 (field number MM075): Cameroon, northeast of Mamfe, Mukwecha, Amebisu, N 05°53.866' E 009°33.495', leg. J. Wurstner & M. Barej, September, 2007.

Paratypes

ZFMK 87694 – 697, 87699 (paratopotypes): Cameroon, Mamfe region, Mukwecha, Amebisu, leg. J. Wurstner & M. Barej, September, 2007.
ZFMK 87700: Cameroon, Mamfe, leg. J. Wurstner & M. Barej, September, 2007.
ZFMK 61243: Cameroon, Korup, Mundemba, leg. C. Wild, February 1989.
ZFMK 51686: Cameroon, Magba, leg. F. Schütte, February 1990.
ZFMK 75376: Cameroon, Mt. Nlonako, Nguengue, leg. H.-W. Herrmann & A. Schmitz, January 2000.
ZMB 55709, 37061: Cameroon, Makum.
MHNG 2713.29 (field number AMC-360): Mofako Balue, Rumpi Hills, Cameroon, leg. locals people, July 2009.
MHNG 2713.30 (field number AMC-248): Big Massaka, Rumpi Hills, Cameroon, leg. M. Barej & A. Schmitz, July 2009.
MHNG 2713.31 (field number AMC-009): Foyer du Marin, Douala, Cameroon, 01.07.2009, leg. M. Barej & A. Schmitz.
MHNG 2713.32 (field number AMC-178): Big Massaka, Rumpi Hills, Cameroon, 09.07.2009, leg. by locals.

Diagnosis. A fairly large species of *Agama* (total length of adult male above 25 cm), which is characterized by a reticulated pattern on the throat, a bright vertebral stripe and a deep blue tail tip in adult males. Males of the new species are distinguishable from all other *Agama*-species by the combination of throat and tail colouration. The throat colouration (fig. 4.1) is a reticular pattern of red lines, which is so far only known from *Agama paragama* (fig. 4.2), *Agama sylvanus* (fig. 4.3) and an undescribed species from Uganda (fig. 4.5). The tail colouration is unique within the genus because of the blue tip of a tricoloured tail (see fig. 2d). Females are similar to those of other species of the *Agama agama* species complex, and can only be safely determined by their genetics.

From southern and eastern African species *A. lebretoni* sp. n. differs as follows:

From *A. planiceps*, *A. turuensis*, *A. mwanzae*, *A. kaimosae* and *A. atra* the new species differs in their unique throat colouration, the blue colouration of the tip of the tail and in having a vertebral stripe. From *A. knobeli* the new species differs additionally in not possessing a tail crest. From *A. mucosoensis* the new species differs in having a red head instead of a yellow. *A. lebretoni* sp. n. is very different in tail colouration (tri-coloured instead of banded narrow white and blue) from *A. lionotus* and *A. kirkii*.

Agama species occurring in Cameroon and Gabon differ from *A. lebretoni* sp. n. as follows:

Agama agama differs in having a black colouration of the tail tip instead a blue one in the new species. Both species also differ in characters of throat colouration: *Agama agama* has a more or less striated to uniform red throat (fig. 4.4), which is dissimilar to the reticulated throat of the new species. *A. agama* is also lacking the typical pale vertebral stripe which is present in nuptial coloured males of

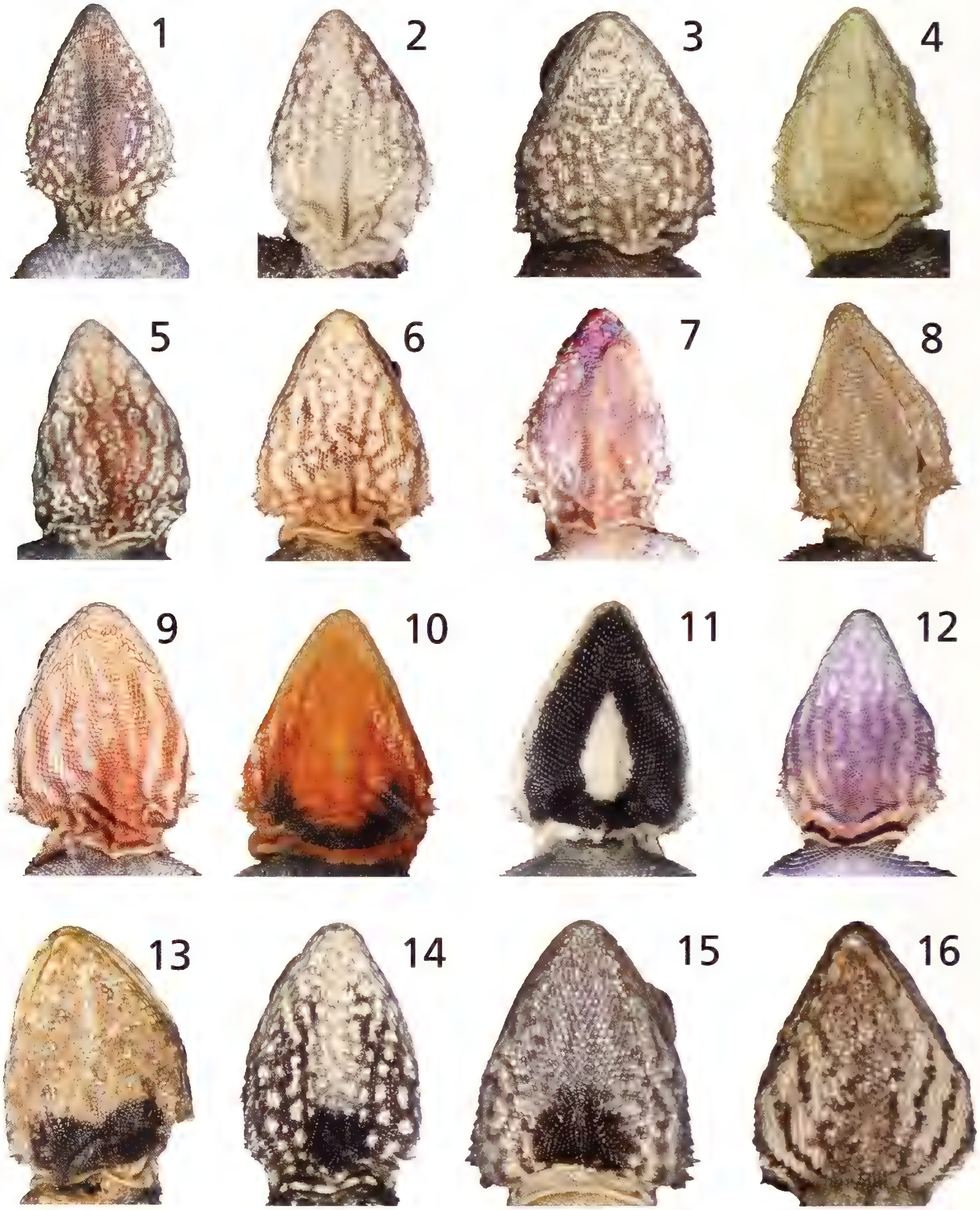

Fig. 4. Throat patterns of some West African adult males of *Agama* species:
1= *Agama lebretoni* sp. n. (holotype, ZFMK 87698); **2**= *Agama paragama* (ZFMK 15244); **3**= *Agama sylvanus* (ZFMK 40252); **4**= *Agama agama* (neotype, ZFMK 15222); **5**= *Agama* sp. n. (ZFMK 88809); **6**= *Agama a. africana* (ZFMK 20125); **7**= *Agama finchi* (NMK L2716); **8**= *Agama planiceps* (ZFMK 55062); **9**= *Agama lionotus lionotus* (ZFMK 83624); **10**= *Agama lionotus elgonis* (ZFMK 82065); **11**= *Agama lionotus dodomae* (ZFMK 83706); **12**= *Agama kaimosae* (NMK L2715); **13**= *Agama doriae benueensis* (ZFMK 29615); **14**= *Agama doriae doriae* (ZFMK 55545); **15**= *Agama sankaranica* (ZFMK 40468); **16**= *Agama gracilimembris* (ZFMK 33719).

the new species. In contrast, *Agama agama* has a slightly lower count of scale rows around midbody. According to GRANDISON (1968) *A. agama* from Nigeria has 59 to 77 rows, whereas *A. lebretoni* sp. n. has 73 to 80 rows [23 specimens].

From *Agama doriae benueensis* the new species differs in having a different throat pattern in dominant males: *A. doriae* with a prominent black dot on the base of the throat (fig. 4.13, 4.14), instead of a reticulated throat in *A. lebretoni* sp. n. Additionally, *A. doriae benueensis* is one of the few *Agama* species which have the nostril below the canthus rostralis instead of on the canthus like in the most *Agama*'s.

Agama gracilimembris is much smaller in size (100 to 120 mm in *A. gracilimembris* in difference to more than 250 mm in *A. lebretoni* sp. n.) and does not have spinose scales around the ear opening as in the most other *Agama* species. Again, also this species differs in the colouration of the throat of adult males: striated in *A. gracilimembris* (fig. 4.16) and reticulated in the new species. In morphology, *A. gracilimembris* differs in possessing strongly keeled head scales and it is also one of the few *Agama* species which have the nostril below the canthus rostralis. However, both species are similar in the count of scale rows around midbody (70 to 85 in *A. gracilimembris* and 73 to 80 in the new species).

From *Agama paragama* the new species differs in possessing a lower nuchal crest, in having a red instead of a yellow-whitish head and in having a higher number of scale rows around midbody (Wagner, unpubl. data). Additionally, adult males of *A. paragama* show a black instead of blue tail tip. GRANDISON (1968) described the colouration of the throat of *A. paragama* (similar to the herein described new species) as 'a dark network on a cream ground which takes the form of isolated, round, cream spots' (fig. 4.2) and as dissimilar to *Agama agama* which has a 'longitudinal arrangement of darker lines or blotches'. However, GRANDISON (1968) also mentioned, that the typical throat colouration of *A. paragama* is present in both sexes, which is not comparable with *A. lebretoni* sp. n.. A similar situation exists in *Agama turuensis* and *Agama lionotus elgonis* which have a very similar colouration of the throat to each other (see fig. 4) but are recognized as distinct taxa by WAGNER et al. (2008a).

Agama sankaranica is completely different in body colouration, but also in other aspects of morphology: this species is much smaller in size and it is one of the few *Agama* lizards which have the nostril below the canthus rostralis. Additionally, *A. sankaranica* has a fewer count of scale rows around midbody (64-78 [69.6] in *sankaranica* versus 73 to 80 [76.2] in *lebretoni* sp. n.) and a very large occipital scale, which is as large as one and half diameter of the tympanum.

Agama lebretoni sp. n. differs clearly from *Agama sylvanus* in having a vertebral stripe instead of a completely blue body in *A. sylvanus*, but both species show a similar pattern of throat colouration in adult males (figs 4.1, 4.3).

Agama lebretoni sp. n. differs from the holotype of *Agama mehelyi* (for comments see below) in having a homogenous body scalation.

From the three other proposed new species mentioned by CHIRIO & LEBRETON (2007) the new species differs as follows: from *Agama* sp. 2 in the larger size; from *Agama* sp. 3 in having the nostril on the canthus rostralis; from *Agama* sp. 4 in having a vertebral stripe and completely blue forelimbs instead of red and blue coloured ones in *Agama* sp. 4.

Comparison of *A. lebretoni* sp. n. with probably valid synonyms of *Agama agama*

Agama colonorum var. *congica* Peters, 1877 was described from Chinchoxo, Cabinda, Angola. One syntype (ZMB 9196) resembles in colouration more *Agama agama*. The typical characteristics of *A. lebretoni* sp. n. (reticulated throat, white speckled body and blue tip of tail) are lacking in this specimen. The other syntype (ZMB 67193) is lacking colouration but shows a relatively large body scalation in difference to *A. lebretoni* sp. n.. It is most probable that *Agama colonorum congica* is a valid species but further investigations are needed.

Agama picticauda Peters, 1877 was described by a series of six syntypes from Ada Foâh in Ghana (Adafer in Mauritania fide LOVERIDGE 1957, which is obviously in error), from Acera in Guinea (= Accra in Ghana?) and from an unknown locality in Cameroon. DENZER et al. (1997) designated the specimen ZMB 403 from Ada Foâh as lectotype. This subadult specimen resembles in colouration and morphology *Agama agama*. Nevertheless, the paralectotype series mistakenly included an adult male of *A. lebretoni* sp. n. (ZMB 8299) from Cameroon. Therefore, because of the chosen lectotype, this taxon must be recognized as synonym of *Agama agama*. Differences between *A. agama* and *A. lebretoni* sp. n. have already been discussed above.

Description of the holotype (figs 1 c–d, 2, 4.1). Habitus stout, snout-vent length (SVL) 140.0 mm, tail length (TL) 199.6 mm, head length (HL) 36.0 mm, head with (HW) 26.0 mm, head height (HH) 15.8 mm.

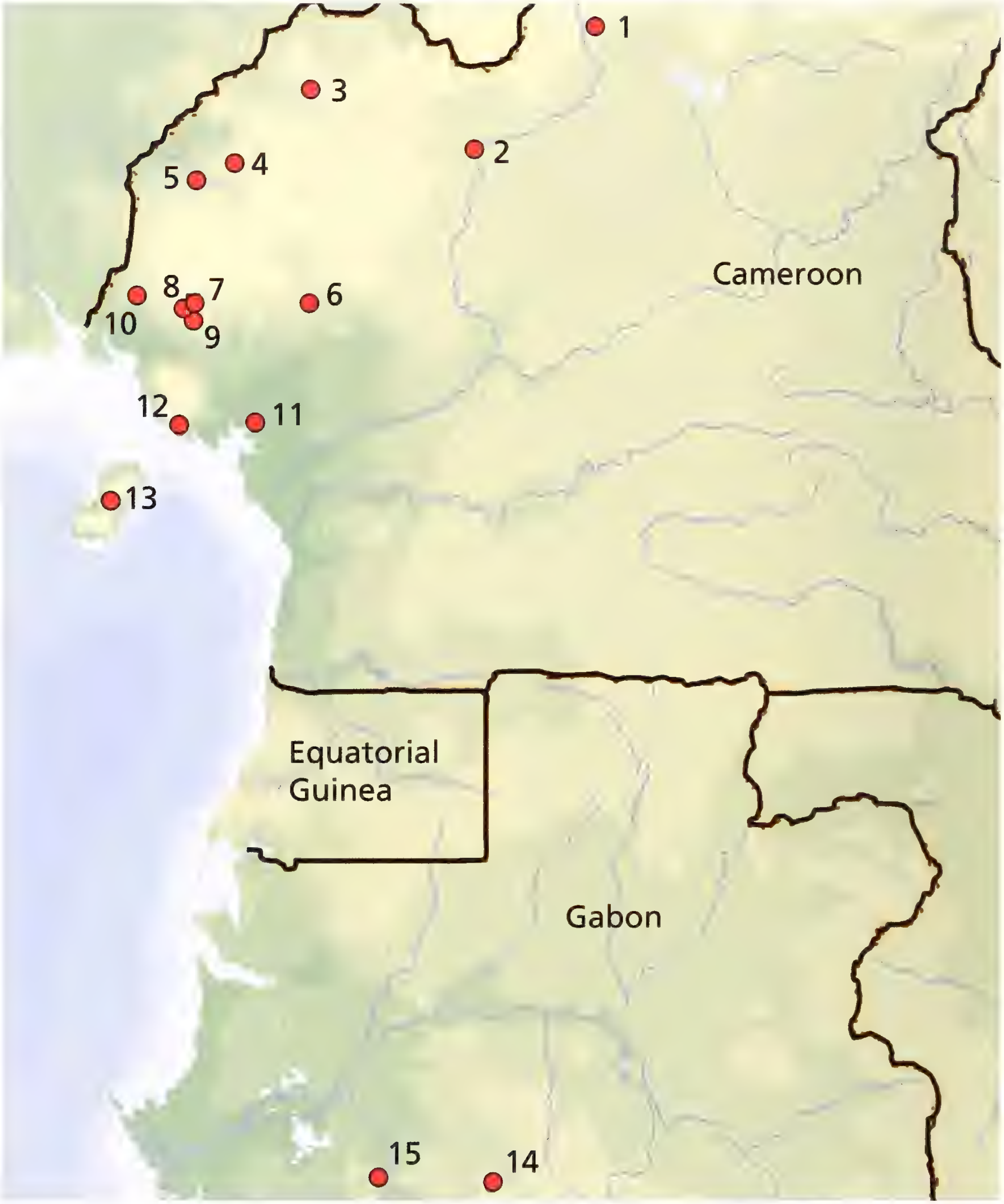

Fig. 5 Distribution of *Agama lebretoni* sp. n. CAMEROON. **1**= Makum (ZMB 55709, 37061); **2**= Magba (ZFMK 51686, 54906 – 907); **3**= Metchum, Wum (ZFMK 15194 – 15200); **4**= Amebisu [=Amebesu] [type locality]; (ZFMK 87694 – 699); **5**= Mamfe (ZFMK 87694 – 699, 87700); **6**= Nguengue, Mt Nlonako (ZFMK 69017); **7–9**= Rumpi Hills: Mofako Balue, Big Massaka (MHNG 2713.29 – 30, 2713.32); **10**= Mundemba (ZFMK 61243); **11**= Douala (MHNG 2713.31); **12**= Limbe (Victoria) (ZFMK 18891 – 894). EQUATORIAL GUINEA. **13**= Bioko Island (Fernando Poo), San Carlos (ZFMK 9353 – 359). GABON **14**= Ngouassa (IRSNB 15686 – 687); **15**= Fougamou (ZFMK 73239 – 245).

Large triangular nasal scale slightly above the canthus rostralis and pierced with the nostril in the posterior part, directed and supplied obliquely upwards. Between the nasal scales, two narrow longitudinal, keeled scales are visible, posterior followed by one smooth transverse scale. Nine supralabial scales, eight sublabial scales on both sides. Head scales between the eyes smooth, directed sideward from a midline between the eyes; head scales between posterior end of the eyes and neck keeled, directed forwards; head scales of the temporal region keeled, directed sidewards; free anterior margins of head scales with numerous sensory pits; supraocular scales smooth. Parietal shield more or less pentagonal, pineal organ visible, pierced in the middle of the shield; parietal shield surrounded by scales more or less equal in size. Ear hole large, about the same size as the eye, margin being composed by spiny scales, surrounded by five tufts (three anterior, two posterior) of more or less spiny, mucronate scales; tympanum superficial. Nuchal crest low, consisting of 17 lanceolate scales. Gular scales flat, smooth, juxtaposed and becoming smaller towards the gular fold. Dorsal body scales strongly keeled and mucronate, equal in size, in 67 scales from midpoint of pectoral region to midpoint of pelvic region. Ventral body scales smooth, slightly imbricate at their posterior margins, in 86 scales from midpoint of pectoral region to midpoint of pelvic region. Together in 79 scales rows around midbody. Tail scales strongly keeled and mucronate. One row of nine precloacal scales. Scales on the upper side of the forelimb strongly keeled, smooth on the underside, on the upper arm scales thrice as large as the dorsal body scales, becoming smaller towards the underside and the manus. 4th finger longest, digital length decreasing 3-2-5-1, subdigital lamellae keeled and mucronate. Scales on the upper side of the hindlimb strongly keeled becoming smooth on the underside, on the upper tights equal in size as the dorsal body scales becoming larger towards the lower tights. 4th toe longest, digital length decreasing 3-2-5-1.

Colouration (in alcohol after 5 months of preservation). Head and neck red. Limbs and body blue, body darker as the limbs. Posterior part of the neck, body and upper parts of the hindlimb speckled with white scales. Between the limbs with a whitish vertebral stripe. Tail at the base blue, followed by white, red and blue. Belly and underside of the limbs blue, tail anterior whitish, posterior bluish. Throat, gular fold and parts of the extreme lower head red with a white speckling, resembles at the throat a reticulate pattern.

Colouration in life. *Males*: head and nape deep red; body and limbs electric to dark blue, body and sometimes upper parts of the limbs speckled white to yellowish; whitish vertebral stripe between the limbs; tail four-coloured: blue (extending from the body), whitish in a transition zone to red and dark blue at the tip; belly and underside of limbs blue; throat with a reticulate pattern of red and white, sometimes more or less red with a white speckling. *Females*: Non-pregnant females and juveniles are vividly coloured. Ground colour is grey-brown, head and forepart of the body blotched with yellow spots, stripes and bars. Body usually with a fine and pale vertebral stripe; yellow and black framed blotches on the lateral parts; along the vertebral zone hexagonal black stripe markings visible; body is also blotched with dark dots and short stripes; sometimes an orange coloured broad stripe on the lateral parts obvious (see fig. 2b). Pregnant colouration of females is clearly different: body becomes uniform brown in ground colour; yellow to orange blotches on head more or less blurred. Body colouration is dominated by broad orange waved or serrated bands (see fig. 2a).

Variation. For some measurements and scale counts in *A. lebretoni* sp. n. see also table 1. Colouration in males and females is variable within the typical pattern of the species and depends on many different factors (see also colouration). Non-dominant males resemble the non-pregnant female respectively juvenile colouration. But also disturbed dominant males can loose their typical colouration rapidly. Dominant males vary in having a distinct or non-distinct vertebral stripe and in the intensity of spots on the body. Females vary in pregnant and non-pregnant colouration. A turnover colouration is unknown.

Etymology. The new species is dedicated to MATTHEW LEBRETON, Yaoundé (Cameroon) in recognition of his contributions to the herpetology of Cameroon.

Distribution. The new species is so far documented by us from Cameroon, Gabon and Bioko Island (= Fernando Poo, Equatorial Guinea) (for details see fig. 5). According to CHIRIO & LEBRETON (2007) *A. lebretoni* sp. n. (=*Agama* spec. 1) is very widespread in western Cameroon. So far only two populations are known from Gabon, but also here a more widespread distribution can be assumed. In Cameroon, the new species also occurs along the western border to Nigeria and therefore an occurrence of *A. lebretoni* sp. n. can be expected for this country.

Relationships. *Agama lebretoni* sp. n. should be closely related to *Agama agama*. As mentioned in this latter introduction this species also occurs in Cameroon with its type locality in the northern part of the country. Both species are very similar in colouration and can be distinguished by the pale vertebral stripe, the white body speckling and the blue tip of the tail in *A. lebretoni* sp. n.

Comments on *Agama mehelyi* Tornier, 1902

TORNIER (1902) described this species on the basis of a single female specimen (ZMB 18149) from Bipindihof which was collected by the botanist Georg August Zenker (1855–1922). Since that time no other voucher of the species was collected or observed. While MOODY (1980), DENZER et al. (1997) and CHIRIO & LEBRETON (2007) listed *A. mehelyi* as valid species none of these authors explained their decision about the validity. WERMUTH (1967) on the other hand stated clearly that he considered the validity of *A. mehelyi* as doubtful. Therefore, the type was examined and compared with other *Agama*-species with a heterogeneous body scalation. From (1) *A. hispida* Kaup, 1827 and *A. etoshae* McLachlan, 1981 the species differs in having a large ear hole. From (2) *A. armata* Peters, 1855 it differs in having no reticulated throat pattern and no strongly keeled dorsal scales. From (3) *A. aculeata* it differs in lacking a network pattern on the central part of the throat. The specimen resembles in scalation and colouration and especially in throat colouration pattern *A. anchietae* Bocage, 1896. Both species show dark wavy strips on the throat. A distinct colouration as in e.g. *A. aculeata* is lacking and both species are characterized by a pale vertebral stripe, four to five cross bands on the body (lacking in the preserved voucher of *A. mehelyi*) and a banded tail. Because of this striking similarities *Agama mehelyi* Tornier, 1902 is considered by us as a synonym of *Agama anchietae* Bocage, 1986.

The locality of the specimen is doubtful. 'Bipindihof' is a well known locality because of the collections made by Zenker on his own plantation. But Bipindihof is a rainforest area where e.g. *Lepidothyris fernandi* (Burton, 1836) (Sauria: Scincidae), a typical rainforest lizard was found (WAGNER et al. 2009a). In Africa, no true rainforest agamid species occur and only species of the genera *Acanthocercus* and *Agama sylvanus* MacDonald, 1981 occur in dense dry forest. Especially the members of the *A. hispida*-group, like e.g. *A. anchietae*, are typical ground dwellers of arid regions. However, between 1889 and 1896 Zenker operated the Post Office of Yaounde and he later moved to Bipindihof to build up a plantation. From 1906 he also operated the Post Office of the area. As a passionate collector Zenker collected ethnographic curiosities, photographs, herbaria, skulls, stuffed birds, mammals, amphibians and lizards. For this collections he probably also used his contacts to the Post Office to get material from other regions of Africa. Therefore, the given locality for *A. mehelyi* is most probably erroneous.

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Appendix. Material examined

Agama agama*:** Senegal. Dakar: Bel-Air: ZFMK 73845-849; Cameroon. Diamaré, Mokolo: ZFMK 15222 [neotype]; unknown locality: ZFMK 83759 – 766. ***Agama colonorum* var. *congica*:** Angola. Cabinda, Chinchoxo: ZMB 9196, ZMB 67193. ***Agama boueti*:** Niger. Agadez: ZFMK 33706 – 714, 36595 – 598; Assaouas: ZFMK 20050 – 051; Dabnou: ZFMK 20051; El Meki: ZFMK 20048 – 049, 20046 – 047; Agadez: ZFMK 20044 – 045. Senegal. Dakar: 17169 – 174; Mboro-sur-mer: ZFMK 17176 – 183. ***Agama d. doriae*:** Ethiopia. Eritrea: ZFMK 20847; Gorgora Land, Lake Tana: ZFMK 19454 – 455; Kaffa, Omo river: ZFMK 15861 – 864. Sudan. Equatoria, Rihi river: ZFMK 29614 – 618; Dinder Parc: ZFMK 38397 – 399; ***Agama doriae benueensis*:** Cameroon. Adamaoua, Martap: ZFMK 15192 – 193; Diamara: ZFMK 15176; Logne et Chari, Waza: ZFMK 15177 – 191; Margui-Wandala, Gouria: ZFMK 20085 – 088, Margui-Wandala, Koza: ZFMK 15175; Margui-Wandala, Mora: ZFMK 8855; Mokolo: ZFMK 33746; Mora: ZFMK 33738 – 745. Central African Republic. Koumbala: ZFMK 33726 – 727; Ndélé: ZFMK 33747, 33728 – 733. Nigeria. Beni Sheik: ZFMK 33734 – 737. ***Agama finchi: Kenya. Malaba: NMK L/2716/1, 4, 6–7, 9–10, ZFMK 83652-656. ***Agama gracilimembris*:** Cameroon. Benoué, Boki: ZFMK 15257 – 259; Benoué: ZFMK 33717. Central African Republic. Koumbala: ZFMK 33718 – 721; Kotissako: ZFMK 33722 – 725. ***Agama kaimosae*:** Kenya: Ngoromosi: NMK L/2715/1, 3–4, ZFMK 83658 – 660; Tanzania: Tanganyika District: Mwamalasa: MHNG 877.65; MHNG 2684.001 – 006. ***Agama kirkii*:** Malawi. Mt. Mlanje: ZFMK 30696 – 697; Zomba: ZFMK 54533 – 534. Zimbabwe. Zimba, Umfuruzi: ZFMK 51254. ***Agama lebretoni* sp. n.:** Cameroon. Douala, Foyer du Marin: MHNG 2713.31; Fako (Mt. Cameroon), Limbe (Victoria): ZFMK 18891 – 894; Korup, Mundemba: ZFMK 61243; Magba: ZFMK 51686, 54906 – 907; Makum: ZMB 55709, 37061; Mamfe: ZFMK 87694 – 699, 87700; Mamfe, Mukwecha, Amebisu: ZFMK 87694 – 699; Metchum, Wum: ZFMK 15194 – 15200; Mt. Nlonako, Nguengue: ZFMK 69017, Rumpi Hills, Mofako Balue: MHNG 2713.29; Rumpi Hills, Big Massaka: MHNG 2713.30, 2713.32. Equatorial Guinea. Bioko Island, San Carlos: ZFMK 9353 – 359. Gabon. Fougamou: ZFMK 73239 – 245; Ngouassa: IRSNB 15686 – 687. ***Agama mehelyi*:** Cameroon: Bipindihof (in error): ZMB 18149 (holotype). ***Agama paragama*:** Cameroon. Logone et Chari, Waza: ZFMK 15242 – 256. Niger. Agadez: ZFMK 36599; Tessaoua: ZFMK 33749 – 750. ***Agama* cf. *paragama*:** Cameroon. Benoué, Boki: ZFMK 15227 – 241. ***Agama picticauda*:** Ghana: Ada Foâh: ZMB 403. Cameroon: ZMB 8299. ***Agama planiceps*:** Namibia. Brandberg: ZFMK 33040 – 041; Frauenstein: ZFMK 18395 – 398; Kaoko, Werda: ZFMK 21961 – 962, Okahandja: ZFMK 2696, 2694 – 695; Omandumba: ZFMK 18399, 33007 – 009; Windhuk: ZFMK 46453 – 456. ***Agama sankaranica*:** Burkina Faso. Ouagadougou: ZFMK 39032. Mali. Kassaro: ZFMK 20053; Monsombougou: ZFMK 20056; Sandaré: ZFMK 20057; Nioro du Sahel: ZFMK 20055. Togo. Lome: ZFMK 40468 – 484, 40525. ***Agama sylvanus*:** Cameroon. Benoué: ZFMK 33751 – 754. Central African Republic. Koumbala: ZFMK 40251 – 260; Mélé: ZFMK 33766; Ndélé: ZFMK 33755 – 7654; Sibut: ZFMK 33765. ***Agama turuensis*:** Tanzania. Mount Hanang: ZFMK 74930 – 943, 82292 – 94, 82324 – 328, 82357 – 360, 82278 – 279.

Appendix

Abstracts of presentations hold on DeAgamis the 1st International Symposium on Agamid Lizards

Oral Presentations

History of Classifications and Phylogenies

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Darwin in his 1859 "Origin of species ..." eloquently demonstrated that taxonomic classifications could (and should) reflect the past evolutionary history of higher taxa and relationships of the extant species. However the major herpetological works, for example, Boulenger's Catalogue of Lizards, published over the next 100 years did not attempt reconstructions of phylogeny. Indeed Boulenger reversed the earlier named (now recognized again) genera and higher taxa proposed especially by W. Peters and L. Fitzinger. Although, Camp (Classification of Lizards, 1923) and Hennig (Revision of *Draco*, 1936) published pioneering works (they were decades ahead of others) the taxonomic herpetologists ignored them until the "rebirth" of phylogenetic systematics in the 1960's and 1970's. Moody (1980) published a phylogenetic analysis based on 122 morphological characters and reviewed the historical biogeography of the agamid genera and proposed several subfamilies. Within the past two decades beginning with Joger (1991, a molecular phylogeny of agamid lizards) several workers have employed molecular analyses. The hypothesized molecular phylogenies by Macey, Larson, Ananjeva, Papenfuss, Ota, Honda, Schulte and Melville will be compared with my original and revised morphologically based hypotheses. The controversy over the familial status of the various higher taxa within the "acrodont" section of the suborder Iguania that ensued following Frost & Etheridge (1989) also will be reviewed.

The arid corridor from Middle East to Africa – Insights from the Agamidae

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The similarities between fauna and flora of the arid southwest and northeast corners of Africa have been pointed out by several authors. E.g. Poynton underlined this distribution pattern of an arid corridor with instances from Bufonid amphibians, whereas Wagner found instances among reptiles, especially agamid lizards. These arid areas are still connected by a strip of arid country through Kenya, Tanzania and northeastern Zambia to southern Africa. This arid corridor allowed a faunal and floral exchange during dry phases of the Quaternary and influenced the colonization history of the continent. The relations and differences between Africa and Middle East are analysed using the agamid taxa *Trapelus*, *Pseudotrapelus*, *Acanthocercus*, *Agama*, *Xenagama* and *Uromastyx*.

Taxonomic, morphological and ecological diversity of Asian agamids (Agamidae:Acrodonta: Sauria:Reptilia)

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One of important aspect of integrative study of lizards of Agamidae family is an analysis of morphological diversity within this group of squamates according to recognizing compositional, structural and functional biodiversity (Noss 1990). Agamidae is morphologically and ecologically diverse family belonging to Iguania that is a sister group to all the remaining squamates (Sukhanov 1961; Moody 1980; Estes 1983, 1985). Agamid lizards are characterized by acro-pleurodont dentition, lack of the intravertebral autotomy fracture plan existing in most other lizards and high structural diversity of integumental derivatives: scale sense organs, epidermal holocrine glands (femoral pores, callose scalation), and so on. We analyze the representation of different evolutionary lines of agamid lizards in Palearctic and Oriental Asia, as well as morphological variety of dentition and integumental structures in these lines. The study of structure and development of dentition revealed a special type of anlage of the egg-teeth in Iguania in comparison with another suqamates (Sergeyev 1940; Ananjeva & Orlov 1986). The single egg-teeth anlage is synapomorphy for Iguania whereas the paired tooth germs are shared by Gekkota, Scincomorpha, Anguinomorpha and all Ophidia. The next developmental transformations lead to paired state of egg-teeth in Gekkota including dibamids (Underwood & Lee 2000) and unpaired (as a result of reduction of one of the two egg tooth germs, or as a result of fusion) state of egg-teeth in another squamates (Ananjeva & Orlov 1986).

Attempts to nest integumental derivats into the phylogenetic tree of acrodonta lizards (Macey et al. 2000; Ananjeva 2004) and to consider association of morphological and ecological diversity of Asian agamids are discussed.

Phylogenetic relationships and evolution of the agamid lizard subfamily Draconinae

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The agamid lizard clade (subfamily) Draconinae is widespread throughout the Indian subcontinent, Southeast Asia, Indonesia, the Philippines, and associated islands of the Indian and Pacific Oceans. Phylogenetic analyses are presented for this clade at several hierarchical levels. Nuclear DNA recover very robust support for the agamid clade Agaminae as the sister taxon to draconines. Within Draconines, relationships are investigated using mitochondrial and nuclear DNA. *Mantheyus phuwuanensis* is strongly supported as the sister taxon to all other draconine species with *Ptyctolaemus* and *Draco* forming a clade that is sister to all remaining species. A detailed phylogeny of Calotes based on mtDNA also will be presented. Finally, the diversification rate of draconine agamids will be compared with *Chamaeleons*, *Agaminae*, and *Amphibolurinae* to identify possible evolutionary important differences between these clades.

Status survey of the Indian Spiny-tailed lizard *Uromastyx hardwickii* in the arid regions of Rajasthan, North-Western India

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The Indian Spiny-tailed Lizard *Uromastyx hardwickii* is endemic to the arid region between India and Pakistan. Known as the ‘Sanda’ in India, it is protected by law (Schedule II, Indian Wildlife Protection Act, 1972). Existing informa-

tion on this species is largely anecdotal and so sparse that the most detailed observations are almost a century old – this species inhabits self-excavated burrows and occurs in clusters; it is believed to be threatened by local trade in its meat and oil, and habitat destruction caused by anthropogenic activities. In order to effectively conserve this unique species basic information such as distribution, location of clusters and habitat characteristics is essential. Therefore, the objectives of this ongoing survey are to map the distribution of the Sanda in the arid regions of Rajasthan (northwestern India), locate large clusters and identify habitats that can support such clusters. In addition, information on threats to the species including extent of exploitation is also being collected. The survey commenced in March and will continue till September 2007: so far, a combination of vehicular transects as well as interviews with locals has been used to assess presence/absence; abundance and habitat parameters have been measured using belt transects. Further, semi-structured interviews with hunting tribes has provided valuable information on exploitation. The survey will also be followed by a more detailed study on the ecology of this species since it is the only herbivorous lizard in the Indian subcontinent.

The genera *Pseudocalotes* and *Bronchocela* in south East Asia: Taxonomy and distribution

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Uncertainty exists about occurrence and differentiation of the species of the genus *Pseudocalotes* in South-East-Asia. The situation in Vietnam and Laos is problematic due to problems in identification, occurrence of different colour morphs or undescribed species. New voucher specimens of that genus from different localities in Vietnam and Laos were examined and compared with type material. A first record of a female *P. poilani* demonstrate sexual dimorphism and differences between *P. poilani* and *P. floweri*. Both species have a restricted distribution to southern Laos (*poilani*) and to southern Cambodia/ Thailand (*floweri*). In Vietnam *P. microlepis* brevipes are more widespread distributed than known. And a third unknonw species occurs in Kon Tum Province /Vietnam. A new species of *Bronchocela* from Nicobar Islands is presented with its variation and distribution. A distribution map for *Pseucocalotes* and *Bronchocela* is presented.

A preliminary phylogeny of the genus *Acanthosaura* Gray 1931, inferred from mitochondrial and nuclear genes

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An analysis of mitochondrial and nuclear DNA from the Southeast Asian lizard genus *Acanthosaura*, was use to asses the phylogenetic relationships of the group. The specimens examined encompass the entire range of the genus, (Myanmar, Thailand, Cambodia, Laos, China, and Malaysia (including its off shore islands, Pulau Tioman, Pulau Aur, Pulau Perhintian, and Pulau Langkawi)) from all seven recognized species. A phylogenteic analysis using parsimony, likelihood, and bayesian analyses was used to test the hypotheses (1) *Acanthosaura* cf. *crucigera* from the Cardamom Mountains forms a distinct group separate from *Acanthosaura crucigera* from its type locality in Thailand (2) *Acanthosaura* sp. from Pulau Aur forms the sister group to other *A. armata*, (3) to see if the Acanthosaura from Pulau Langkawi is more closely related to the Cambodia's *A.* cf. *crucigera* then from the type locality in Thailand, following other biogeographic patterns. This will be the first time all recognized species will be included in a phylogenic context.

Who's who – The Specific status of *Leiolepis belliana* and *Leiolepis reevesi*

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The taxonomy of the lizard genus *Leiolepis* has long been problematic. Much of this is seeded in the high degree of morphological variation in the two most wide spread species, *Leiolepis belliana* and *L. reevesi.* To date all studies involving these species have use specimens from the distant ends of their distribution adding to the evidence that these species are distinct from one another. Through recent collection efforts at the contact zone of these species in southern Indochina, has produced morphological data suggesting that these two species are conspecfic and morphologically grade into one another. A phylogenetic analysis of mitochondrial and nuclear DNA was preformed to test the hypothesis of these two species representing one species. This would indicate that all other species of *Leiolepis* have arisen from one wide-ranging species.

Australian Agamid Lizards: an overview of species diversity, biogeography and evolutionary relationships

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Approximately 70 species of Agamid lizards are currently recognised in Australia and are known as the sub-family Amphibolurinae, which is genetically distinct from other agamid clades. Over the last decade we have undertaken a revision of the systematics of this subfamily, using molecular and morphological techniques. We have completed DNA sequencing of more than 2000 individuals for mtDNA and the nuclear region RAG1. I will be presenting an overview of these results. We have found that species diversity is underestimated in the current taxonomy, particularly in the genera *Diporiphora* and *Tympanocryptis.* In addition, these two genera show distinct geographic centres of species diversity, with multiple sympatric species – *Diporiphora* in north-western Australia and *Tympanocryptis* in north-eastern South Australia. The genetic structuring across arid and semi-arid Australia is highly complex in the genera *Diporiphora, Tympanocryptis, Amphibolurus* and *Lophognathus*, with greater levels of genetic divergence than expected. Our results will provide important insight into evolutionary patterns, historical biogeography and speciation in arid and semi-arid Australia.

Viviparity in the family Agamidae

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When Moody (1980) reviewed reproductive mode within the family Agamidae only two clades were known to be viviparous. *Cophotis ceylanica* is viviparous although the other two closely-related genera (*Lyriocephalus* and *Ceratophora*) have oviparous species. The genus *Phrynocephalus* has several viviparous species although others are oviparous. Surprisingly none of the desert-adapted amphibolurines of Australia are viviparous. The family Chamaeleontidae has both oviparous and viviparous clades and since this family is arguably embedded cladistically within the family Agamidae *sensu lato*, the paucity of viviparity within the large radiation of agamids (Draconinae Moody) in southeastern Asia is enigmatic. I was pleasantly surprised when Bjorn Lardner recently sent to me photographs of a female agamid with a full-term fetus collected in Borneo. Thus a third case of viviparity has been documented *Hylagama borneensis* Mertens. I will review the evolution of viviparity within the agamids in light of ecological and physiological adaptations and restraints, and speculate as to why viviparity has not evolved more frequently within the Agamidae.

POSTER PRESENTATIONS

On Systematics and phylogeography of sun watcher toad agamas *Phrynocephalus helioscopus* (PALLAS, 1771)

Daniel MELNIKOV[1], Natalia B. ANANJEVA[1], Mehdi RAJABIZADEH[2] &
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Results of our study on historical background and taxonomic status of two Iranian-Transcaucasian forms – *Phynocephalus persicus* DEFILIPPI, 1863 and *Phynocephalus helioscopus horváthi* MÉHELY, 1894 was showed recently (MELNIKOV et al. 2008). Results of our current study on toad agamas of *helioscopus*-group from whole species range with the same mitochondrial marker (ND2, 700 bp) and its congruence with morphology are presented.Two main lineage – Iranian-Transcaucasian and Turanian – were detected on molecular analysis data. Specimens from southernmost locality Abadeh (Southern Iran, Zagros mountains) occupy basal position in Iranian-Transcaucasian lineage. Apical positions in this lineage have specimens from Saveh (Central Iran, type territory of *Ph. persicus*) and specimens from Aralik (Turkey, type territory of *Ph. h. horváthi*), Armavir (Armenia), Iughli (north-western Iran). These two forms also have good morphological differences in distance between nostrils and L/Lcd ratio (Melnikov et al., 2008). Contrary to our previous opinion about *horváthi* as a form of Turanian lineage, now we have strongly supported data that it belongs to Iranian-Transcaucasian lineage. Basal position of agamas from Charyn and Taskarasu (south-eastern Kazakhstan, left bank of Ili River, near to type territory of *Ph. h. cameranoi* BEDRIAGA, 1907) is most surprising in Turanian lineage. Other lizards from the south-eastern Kazakhstan (Otar, Burylbaital, Ay, Panfilov) are clustered with agamas from Fuyun (western China, type territory of *Ph. varius* Eichwald, 1831) and occupy apical position in this lineage. Specimens from Baskunchak, Tautobe (south-eastern Russia, Astrakhan region) and Akespe, Kamyshlibash (western Kazakhstan, Aral Sea) have another apical position in this lineage. Type territory of *Ph. helioscopus* (PALLAS, 1771) is situated between these two areas. Phylogenetic positions of specimens from Kagan and Tamdy, Eddum (southern Uzbekistan) are not clear because of scanty material. Agamas from supported clades demonstrate some difference in morphology. *Ph. h. helioscopus* specimens have jet-black tip of tail, that easy to distinguish even on old collection material. Coloration of lower surface of tail end in males *Ph. h. helioscopus* is ensanguined, in *Ph. h. varius* is vinous, in animals from Charyn and Taskarasu is orange-red. This red coloration is fast to disappear in collection specimens. Morphological features suitable for identification of collection material are working out.

Distribution patterns of agamids in the North Caspian region

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Five species of agamid lizards (*Trapelus sanguinolentus, Phrynocephalus mystaceus, Phrynocephalus helioscopus, Phrynocephalus guttatus, Phrynocephalus interscapularis*) occur in the North Caspian Region. *Phrynocephalus mystaceus* and *Phrynocephalus guttatus* are psammophilous species and they demonstrate a wide north-caspian distribution in the Caspian Depression reaching the Ergeni Hills in the west and Terek-Kuma Sands in the south. The northernmost agamid species, *Phr. guttatus*, is distributed in the Sarpa Depression in the north. The sclerophillic *Phr. helioscopus* occupies only eastern part of the Caspian Depression from the Western Kazakhstan in the east to the Volga River in the west. In the European part of the range this species is distributed sporadically and very rare. *T. sanguinolentus* demonstrates Caucaso-Middle-Asian range disjunction and inhabits the Terek-Kuma Sands in the west and eastern extremity of the Caspian Depression in the east. *Phr. interscapularis* is represented by an isolated relic population in the Caspian Karakum Desert. Three types of distributional patterns could be distinguished for agamids in this region:

1. continiuous north-caspian distribution (*Phr. mystaceus, Phr. guttatus*),
2. disjunctive north-caspian distribution (*T. sanguinolentus*),
3. relic north-caspian distribution (*Phr. helioscopus, Phr. interscapularis*).

Phr. interscapularis is an endemic species of the Middle Asian and the East Iranian deserts. *T. sanguinolentus, Phr. helioscopus* and *Phr. mystaceus* have Middle-Asian ranges and were described as a subendemic species of the Middle Asia and the Eastern Iran. The wide distributed in the Middle and Central Asia, *Phr. guttatus* has possibly Central-Asian origin. Two species in the North Caspian Region are represented by Turanian subspecies (*Phr. h. helioscopus* and *Phr. i. interscapularis*). A subspecific endemism are known for three species of agamids in the North Caspian Region. *Trapelus sanguinolentus, Phrynocephalus mystaceus* and *Phrynocephalus guttatus* are represented here by endemic subspecies (*T. s. sanguinolentus, Phr. m. mystaceus, Phr. g. kalmykus*). In the territory of the Middle Asia these species are represented by Turanian subspecies (*T. s. aralensis, Phr. m. galli, Phr. g. guttatus*).

This work was supported by the grant of Scientific School N° 4212.2006.4.

Phylogeography & taxonomy of the Agamid lizards (Sauria: Agamidae) of East Africa: morphological and genetic analysis

Alexander Burmann, Philipp Wagner, Bernhard Misof, Martin Haase & Wolfgang Böhme

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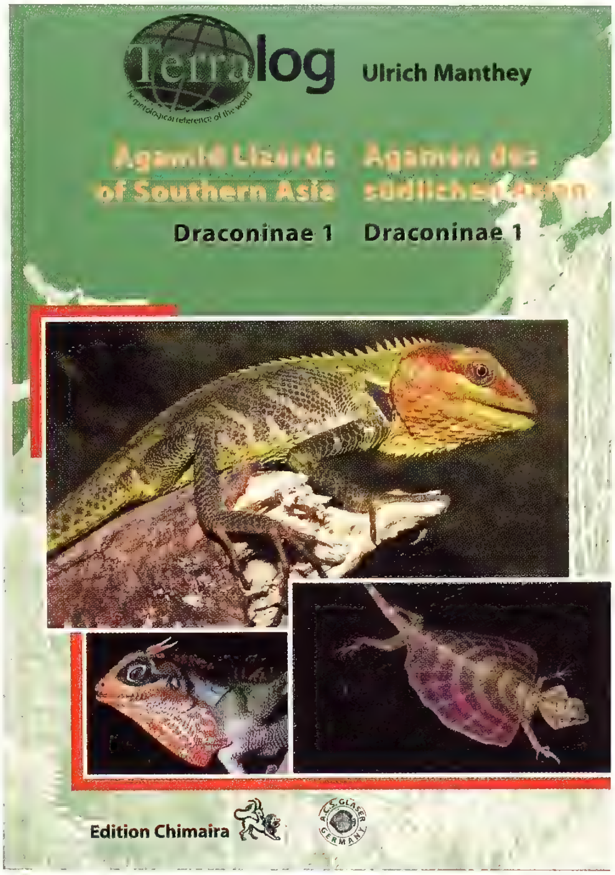
The East African members of the *Agama lionotus* complex are analyzed. The results clearly show differences in morphology and colouration between the *A. lionotus* subspecies. Especially the throat of adult males is a characteristic to determine the different species and subspecies.

MANTHEY, Ulrich (2008). Terralog Vol. 7a – Agamid Lizards of Southern Asia, Draconinae 1. Edition Chimaira, Frankfurt am Main / Rodgau. 160 S., Hardcover. ISBN 978-3-89973-357-0.

This first part of the volume 7 of TERRALOG portrays 95 agamid species of the subfamily Draconinae from Asia.
All species are roughly described with pictograms only (without text) and with a distribution map including the type locality. This book contains the most beautiful photo collection of agamid lizards of southern Asia that I have ever seen. Usually adult males, females and juveniles are figured for all species (often from more than one locality), totalling in more than 530 colour figures. The book not only pays deference to the tremendous colour variation of individuals in some of the treated species, but also to the great species diversity of this subfamily (species lacking in this book will be published in the second part of the volume). Additionally, for some species also the holotype or the habitats are illustrated. Most of the images are from the author himself but several other well-known agamid reserchers contributed images, e.g. J. McGuire, L. L. Grismer, W. Böhme, T. Ziegler or N. Orlov.
In the introduction the genera and some of the species are characterized (though not very exhaustive) and in some cases detailed information about the current taxonomic status (e.g. *Draco abbreviatus*) is considered as valid, or the distribution are given. These data include new findings, e.g. a first record of *Japalura tricarinata* for Tibet. The introduction includes also a part 'How to use the book', some information on husbandry of species and a list of bibliographical references. The text comes bilingual in English and German.
Summarizing, the book is not a taxonomic, ecological or naturalists' guide, but a perfect photographic account for professional and amateur herpetologists who are interested in the family Agamidae in general, or more specifically in the subfamily Draconinae.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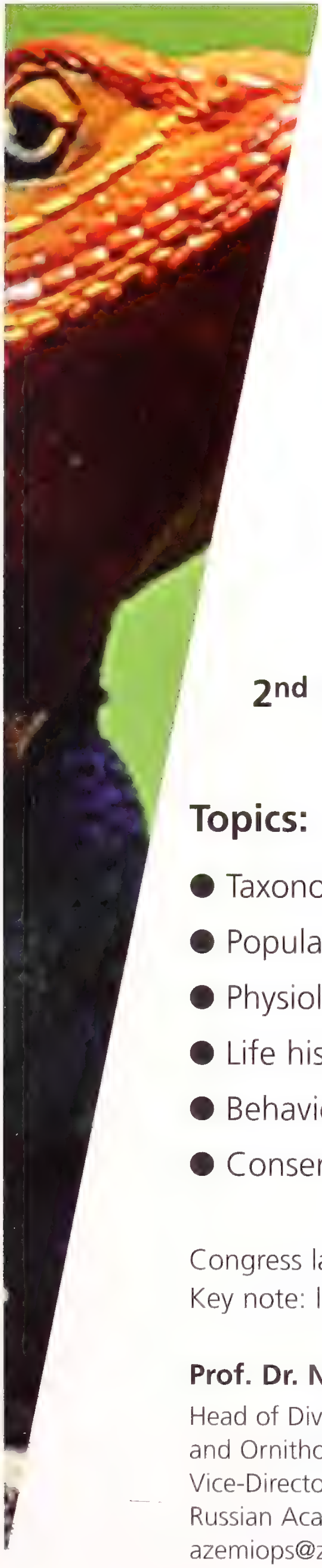

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Scopoli, I. A. 1763. Entomologia Carniolica. I. T. Trattner, Vienna.

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Titelbild/Cover illustration:
Agama planiceps Peters, 1862 from Namibia. Photo by Dieter M. Humbel.

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